Investigating Neural Substrates of Visual Motion Sensitivity in Deaf Individuals

Alexandra Toba Levine

Doctor of Philosophy

University of York
Psychology

July 2017

Abstract

The aim of this thesis has been to explore neural substrates of enhanced far-peripheral visual motion processing in congenitally deaf adults. To do this, psychophysical measures were used as well as novel fMRI stimulus delivery methods to record responses to stimulation in the far-peripheral visual field.

For the first time, far-peripheral visual field mapping measured an extended representation of the visual field (72 °) in early visual cortex in deaf and hearing individuals. Using this method, unique evidence of plasticity within the cortical surface area distribution of visual field representations in the primary visual cortex was found in congenitally deaf adults, biased towards the far-peripheral visual field.

Furthermore, neural responses to far-peripheral stimuli were measured in visual motion processing areas V5/MT+ and V6, and in auditory regions. Results show novel and distinctive differences in response profiles in auditory, but not visual regions between deaf and hearing participants, indicating crossmodal plasticity in deaf participants, specific to coherent but not incoherent global optic flow field motion stimuli.

Most importantly, the aim of the thesis was to relate neural measures to behavioural performance of motion perception. The results show evidence that unimodal plasticity in V1 and activation in visual motion areas V5/MT+ and V6 are not related to performance in two visual motion tasks (local motion detection and global motion direction discrimination), but that response inhibition and excitation levels in auditory regions are related to motion processing performance in deaf and hearing individuals.

In summary, the findings described in this thesis show for the first time that congenital deafness leads to plastic changes within primary visual cortex. In addition, auditory but not visual motion regions are recruited differentially between deaf and hearing individuals, depending on the motion type, and this activation shows a trending relationship with visual motion performance in both groups.

Contents

List of Tables

List of Figures

Acknowledgements

Firstly, I would like to extend my gratitude to my supervisor, and 'science-mum', Dr Heidi Baseler. I want to thank you for the endless enthusiasm, knowledge and encouragement you have given me throughout the past five years. Thank you for believing in me, and making sure I got the hint and applied for the PhD studentship with you. I also want to thank Prof Antony Morland and Prof Alex Wade for constructive discussions and guidance during our TAP meetings. I want to thank Dr Mark '*Hymatron*' Hymers and Dr Andre '*Gouwsed*' Gouws for their help and fruitful discussions, be it at YNiC, St. Petes beach or the pub. I am also very grateful for all the countless words of encouragement from all the PI's at the department. I also want to thank Dr Charlotte Codina and Dr David Buckley of Sheffield University for their valuable collaborative input and useful discussions.

I am extremely grateful for the opportunity to do my MSc in Cognitive Neuroscience and Neuroimaging here at York, which led me to my PhD. I could not have wished for a better place and department to be part of. Thank you to everyone at YNiC, for making it my science home, for the support and encouragement, and collaborative feeling where no question was stupid.

Alongside the incredible academic support, I could not go without mentioning all the aspects surrounding my doctorate here in York.
Words cannot fully describe how grateful I am to my fellow PhD friends, for such limitless support. I especially want to thank Lucie, Tom, Alec, Babs, Ellie, Jet, Eilidh, Ryan, Milena, Sarah, *The Little Boy*, Christin and the Morland lab for your support, words of advice and endless listening capacity. Also, to the nights out with the green chemists, yoga sessions with Rob and Yoga Soc, bake-off dinners and my bottomless supply of Brew York beer; you kept me sane. To the sports village gang where a bad day at the office

was quickly forgotten and left outside of Studio 1; you saw me through a regular weekday and supplied me with endless fun. Without you all, completing this PhD would have been much, much harder.

Most of all, I want to thank my family for being the biggest source of strength, comfort, encouragement and support. Thank you Mum for making me believe I was capable of achieving anything I put my mind to. To my brothers, Adam and Jakub, thank you for your constructive discussions and for boosting my confidence when I needed it most.

Declaration

I declare that the work presented in this thesis is original and my own, and was carried out under the supervision of Dr Heidi Baseler. This work has not been submitted to this or any other University for a degree. All sources are acknowledged as References. Some of the data collection was carried out as part of MSc projects, the first which I was part of during my MSc course in Cognitive Neuroscience, and the second which I co-supervised as a PhD student: data included in Chapters 3, 4 and 5 were collected jointly over the two projects by myself, Laura Bridge, Sally Clausen, Shradha Billawa, Eleanor Cole, Shanelle Canavan, Vera Wang and Lucy Spencer. Dr Charlotte Codina and Dr David Buckley both contributed in the form of participant recruitment for all projects included in this thesis. Findings described in this thesis were presented in preliminary form as the following:

Data from **chapter 3 and 5 and 6** was included in a poster presented at the annual meeting of the European Conference on Visual Perception, Liverpool, UK, as:
Levine, A., Codina, C., Buckley, D., De Sousa, G., & Baseler, H. (2015, August). Visual performance linked to cortical magnification differences in deaf and hearing adults. *PERCEPTION*, 44, 337-337).

Data from **chapter 3** was included in a poster presented by Dr Heidi Baseler at the annual meeting of the European Conference on Visual Perception, Liverpool, UK, as:
Baseler, H., Codina, C., Buckley, D., Campbell, C., De Sousa, G., & Levine, A. (2015, August). Differences between deaf and hearing adults in visual projections from eye to brain. *PERCEPTION,* 44, 303-303.

Data from **chapter 3 and 5 and 6** was included in a Poster presented at the annual meeting of the Vision Science Society, St-Petes Beach, FL, as:

Levine, A., Codina, C., Buckley, D., De Sousa, G., & Baseler, H. (2015, May). Differences in primary visual cortex predict performance in local motion detection in deaf and hearing adults. *Journal of vision,* 15(12), 486-486.

Data from **chapter 4, 5 and 6** was included in a Poster presented at the annual meeting of the Vision Science Society, St-Petes Beach, FL, as:

Levine, A., Billawa, S., Bridge, L., Clausen, S., Hymers, M., & Baseler, H. (2014, May) FMRI correlates of visual motion processing in hearing and deaf adults. *Journal of Vision*, 14 (10), 297-297.

Data from **chapter 4, 5 and 6** was included in a poster presented at the annual Applied Vision Association AGM meeting, York, UK, as:

Levine, A., Billawa, S., Bridge, L., Clausen, S., Hymers, M., & Baseler, H. (2014, April). The role of visual motion areas in global motion integration in deaf and hearing adults. *PERCEPTION*, 43 (5), 474-475.

Chapter 1

Background

As the world is inherently multisensory- visual, auditory and tactile inputs are processed simultaneously in order to provide an internal depiction of the outside world. Our capacity to interact with the world relies heavily on our cognitive systems ability to use and integrate these multisensory signals. Vision plays a crucial role in providing information about the spatial layout of a scene, as well as events and objects within it. Although the visual field is able to provide a substantial amount of input, a large proportion of the surroundings remain unknown. This is where distal senses such as tactile, olfactory and auditory signals can provide sensory input beyond the boundaries of visual perception. Auditory signals in particular, are able to provide precise spatial information on localising non-visible stimuli, thereby demonstrating their importance in guiding the reorientation of the visual system (Heffner and Heffner, 1992)

A fundamental area that has long been investigated by scientists is the consequence of sensory loss, with respect to both blindness and deafness, and how these changes in perception affect the remaining senses. A common view assumes that the absence of one sensory modality will result in changes in the remaining and intact senses. Two opposing theories can be used to explain possible results of sensory loss. An early account described by James (1890) postulated that if a sensory input is lost, the remaining ones become heightened, as a larger reliance is placed on them. As a result, in a sensory deprived group, this leads to better performance compared to average individuals, a phenomenon known as 'hyper-compensation (Röder and Neville, 2003). This leads to the idea of cross-modal plasticity, where a region of the brain deprived of signals from one sense can be

recruited for processing signals from the remaining senses.

A related 'sensory compensation hypothesis' discussed by Gibson (1969) also postulates the idea that the remaining senses compensate to enhance processing. Here, the concept of functional reallocation is introduced whereby neural architectures, specifically the brain areas serving the sense which is impaired, may develop the ability to process sensory input from the intact sensory modalities. Alternatively, it is also possible for the neural areas processing the intact senses to develop enhanced processing capabilities. Behaviourally, this can be seen when the congenitally blind show enhanced pitch discrimination abilities compared to sighted individuals (Gougoux et al., 2004). Furthermore, neural effects of blindness result in an increase in representation of different pitches in the auditory cortex (Elbert et al., 2002).

A theory opposing the compensatory account, namely the perceptual deficit hypothesis (Myklebust, 1960) hypothesises that when one sense is lacking the remaining senses are underdeveloped and proposes that multisensory learning is essential for the full development of each sensory modality. Here, a lack of compensation is thought to lead to reduced performance within intact sensory modalities relative to healthy individuals. For example, deaf children showed a deficit in a texture segmentation and visual search task (Rettenbach et al., 1999). Such an effect illustrates the necessary contribution of a given sense which is lost and subsequently reflected in the diminished performance of intact senses.

When investigating the effects of sensory loss, it is important to consider the plastic capabilities of the brain, which can have both negative and positive effects. Indeed, it is possible that both the sensory compensation and sensory deficit hypotheses are not mutually exclusive, with outcomes determined by the point at which a given sense is lost in ones lifetime. There is considerable evidence for critical phases during development where heightened cortical plasticity is observed which may compound the effects of ongoing experience (Hensch, 2005; Knudsen, 2004). Accordingly, in the case of deaf people, these periods may in turn affect the brain differently depending on when hearing loss was acquired. As it is difficult to dissociate between the effects of plasticity following sensory loss and critical periods during development influencing cortical plasticity, the early deaf population provides a unique means to investigate brain plasticity in the complete absence of auditory stimulation.

1.1 Visual system

The visual cortex is a highly-mapped and well-understood part of the brain (Tootell et al., 1995), guided by primate as well as feline studies (Felleman and Van Essen, 1991). Visual information is processed by an estimated 50-60% of the cortex. When light enters the eye, the lens focuses light onto the back of the eye, the retina, which triggers photoreceptive cells. These signals are then sent through the optic nerve to the lateral geniculate nucleus (LGN) to the visual cortex. The general organisation of the visual cortex displays a gradient between central and peripheral visual field processing where the central (also referred to as foveal) representation is highly magnified. Here, a disproportionate over-representation of the central retina, in contrast to the under-represented periphery, is reflected in the number of afferent neurons from respective retinal regions. This organisation principle is referred to as the cortical magnification factor, defined as the linear extent of visual striate cortex to which each degree of visual angle the retina projects to (Cowey and Rolls, 1974).

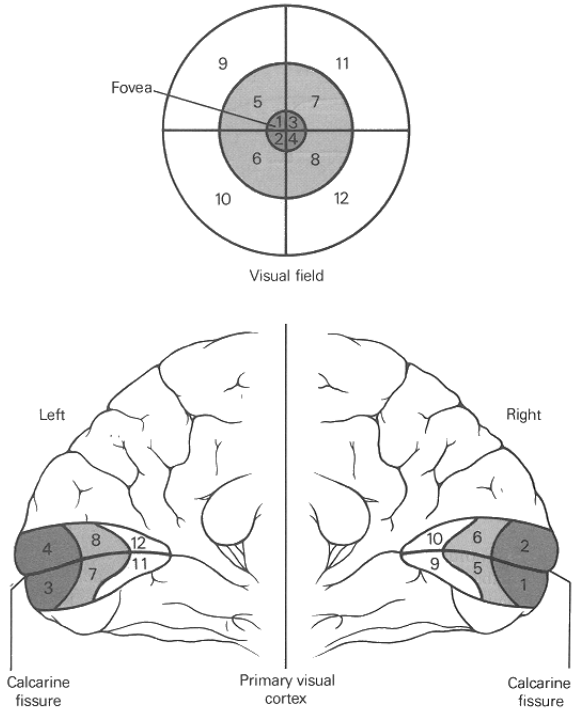

Figure 1.1 – Representations of the visual field as reflected in primary visual cortex. Source: http://fourier.eng.hmc.edu/e180/lectures/v1/node3.html

To provide a comparison, 1 mm^2 of the retina which represents the central 10 $^\circ$ of vision, or 5.5% of the total visual field, is processed by around 60% of the striate cortex, as demonstrated in Figure 1.1. The remaining part of the visual cortex is devoted to processing the peripheral visual field. The central visual input possesses high spatial resolution, with finely grained, smaller receptive fields (Levi et al., 1985; Engel et al., 1997, smaller than a cone diameter,) whilst the periphery possesses poorer resolution, larger receptive fields and a high sensitivity for motion (McKee and Nakayama, 1984). Receptive fields refer to the sensory space to which a neuron responds to. In regards to the visual system, a receptive field is the portion of the retina which is activated by a particular section of the visual field (Hubel and Wiesel, 1962). This is also mirrored in the fact that sensitivities to velocity moves from slow to fast at larger eccentricities, as shown by studies of the cat visual system (Walsh and Polley, 1985). A high number of Y-type motion sensitive neurons are present in the peripheral retina, which in turn project to the peripheral representation within primary visual cortex (Cleland and Levick, 1974).

1.2 Functional organisation of the visual cortex

There are many distinguishable visual areas within the brain, which play their own specialised part in the perception of the visual world (Zeki et al., 1998). Two distinguishable visual processing streams largely define this organisation, the dorsal and ventral stream. The dorsal stream guides our interactions with the surrounding environment, such as reaching and grasping, and this stream leads from V1 to the posterior parietal cortex. The ventral stream is tuned to the perception of objects, faces and scenes in our environment, and this stream leads from V1 and extends to the temporal lobe. Anatomical and physiological evidence suggests differences in central and peripheral visual field representations within the two visual streams. The dorsal lateral geniculate nucleus (LGNd) where central vision is represented more by parvocellular layers than magnocellular layers, the parvocellular layer declining faster as a function of eccentricity than do those of the mangocellular layers (Connolly and Van Essen, 1984). Furthermore, sub-regions within the ventral stream include receptive fields which encapsulate foveal regions more so than peripheral regions, whilst subregions within dorsal stream have receptive fields representing central and peripheral visual fields more evenly (Duhamel et al., 1998). This suggests that cortical magnification extends through the ventral 'what' stream, where object iden-

tification requires a larger proportion of foveal emphasis, whilst the dorsal 'where' stream has an equal proportion of emphasis. This distinction is relevant, as plasticity in the deaf population is largely seen in regions of the dorsal stream, involving the visual periphery.

1.3 Visual field mapping in fMRI

A widely utilised approach which can be used to investigate cortical plasticity within the visual cortex is functional magnetic resonance imaging (fMRI), which can determine direct neural substrates of behaviour. By mapping visual field representations it is possible to identify visual areas influenced and re-organised as a result of auditory deprivation.

A widely utilised approach which can be used to investigate cortical plasticity within the visual cortex is functional magnetic resonance imaging (fMRI), which can determine direct neural substrates of behaviour. By mapping visual field representations it is possible to identify visual areas influenced and re-organised as a result of auditory deprivation.

FMRI makes it possible to measure cortical activation indirectly through the blood oxygenation level dependency (BOLD) signal, which quantifies changes in magnetic properties between oxygenated and de-oxygenated blood surrounding neuronal activity in a given brain region. Visual field mapping in fMRI makes use of BOLD and allows for the localisation of visual field representations in the cortex. This is done by using visual stimuli such as a rotating and expanding flickering checkerboard which progress gradually through the visual field which allows the identification of representations of polar angle and eccentricity. For example, the expanding ring stimulus illustrated in Figure 1.2 measures the retinotopic organisation of visual areas in respect to visual field eccentricity. As the expanding ring is delayed in the peripheral visual field relative to the centre, the temporal phase of the travelling wave of responses varies as a function of distance from the central visual field, cortical responses moving from posterior to anterior occipital cortex. Thus, it is possible to systematically map out which portion of cortex is dedicated to processing the corresponding part of the visual field, as can be seen in Figure 1.2. Based on the same principle, the rotating wedge stimulus probes the retinotopic organisation of visual areas in relation to polar angle, which enables the identification of hemifield and quarterfield representations of visual space. The wedge rotates around the central fixation point, this way periodically activating neurones along the direction of the rotation. The BOLD ac-

tivation values are correlated with a reference function derived from the time course of the retinotopic stimulus presentation. fMRI responses are quantified as the phase and amplitude of the sinusoid that best fit the average time series of voxel response within the visual cortex (DeYoe et al., 1996; Engel et al., 1997; Sereno et al., 1995).

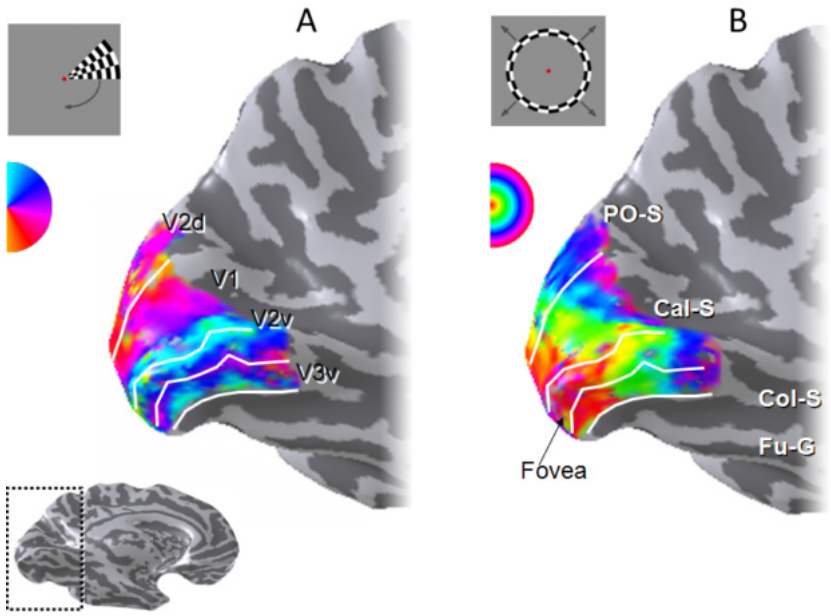

Figure 1.2 – Travelling wave stimuli displayed on an inflated left hemisphere surface. The rotating wedge stimulus (A) represents the response phase at each polar angle location and the expanding ring stimulus (B) maps the phase response of eccentricity. Boundaries of visual areas are indicated by white lines, V1 is located in the calcarine sulcus (Cal-S) with dorsal and ventral V2 on either side, V3 following the same organisation. Figure is from Brewer and Barton (2012)

The travelling wave method has successfully identified 20+ visual areas (Wandell et al., 2007). Primary visual cortex, V1, occupies the calcarine sulcus and represents a hemifield of visual space, i.e it is retinotopically organised, a layout which refers to the fact that afferent connections from the retina hold their organisation through sub-cortical structures. The transfer of visual input can be seen from the LGN to V1, where it then transforms this information, sending it to secondary area, V2. V2 then distributes this signal further up the visual hierarchy (Livingstone and Hubel, 1988). Taken together this methodology allows us to identify, measure and compare attributes of visual field maps present in the brain.

1.4 Audio-visual connections

As visual organisation of the cortex is considered, the senses complement each other by collating initially disparate pieces of perceptual information. To this end, cross-modal effects can be found between visual and auditory cortices in primates, as the two sensory regions have been shown to be anatomically interconnected; monkey visual cortex receives a large number of neural projections from sections of auditory cortex from areas coding auditory spatial information (Rockland and Ojima, 2003). The non-human primate auditory cortex also sends projections primarily to areas of the visual cortex responsible for processing peripheral visual space (Falchier et al., 2002). These direct connections within the monkey brain demonstrate the interdependence of the modalities, which in turn strongly suggests that a similar neural architecture is present in the human brain.

Some of the numerous behavioural examples that show the interactions between the sensory modalities include perceptual illusions, such as spatial ventriloquism, where a sound is mislocalised towards a temporally matched yet visually displaced event, as well as the McGurk effect (McGurk and Macdonald, 1976) where the perception of syllables is fused between the auditory and visual perception of lip movements (Macaluso and Driver, 2005; Spence, 2011). Auditory stimuli can also drive the spatial perception of visual stimuli, leading to the overestimated perception in visual localisation (Recanzone, 2003). These examples showcase the interaction of sensory modalities and how they lead to our perception of the multisensory world.

1.5 Auditory deprivation and visual compensation

How does the brain adapt when input from one sensory modality is lost? In congenital deafness the interaction between auditory and visual sensory modalities are not available, and the ramifications on visual perception are a subject of ongoing research with the interconnections between the visual and auditory senses measured through behavioural experiments and neuroimaging. Importantly, the latter methodology enables further investigation into the impact of congenital deafness on visual function and its neural markers.

Behavioural and brain imaging studies by a number of research groups have repeatedly

shown that lack of auditory stimulation does indeed influence visual processing (Neville and Lawson, 1987; Loke and Song, 1991; Bavelier et al., 2000; Proksch and Bavelier, 2002; Stevens and Neville, 2006; Hauthal et al., 2013; Heimler and Pavani, 2014; Shiell et al., 2014; Codina et al., 2017). However, it is not simply a case of superior or inferior visual processing abilities in deaf individuals, but rather a case of selective enhancements within visual processing compensating for what would have otherwise been processed by the auditory modality. Motion processing, specifically within the peripheral visual field, shows the strongest enhancement in congenitally and profoundly deaf adults in this regard (Bavelier et al., 2000; Stevens and Neville, 2006; Buckley et al., 2010; Hauthal et al., 2013). It is not by chance that the observed sensitivity emerges within large eccentricities. Peripheral vision is used to monitor the surrounding environment for changes and hazards, and normally benefits from the simultaneous context provided by auditory and visual modalities. In the absence of the auditory input, peripheral vision can compensate for the lack of cross modal integration.

To test possible effects of sensory deprivation on visual processing, Loke and Song (1991) investigated differences between hearing and deaf subjects in visual target detection tasks, and found that the deaf subjects were faster at detecting target stimuli in the periphery (25 °), corroborating the predictions made by the sensory compensation hypothesis. The reaction times were equivalent within the central visual field (0.5 °) for both groups; however, the experimental task was not ideal to measure central sensitivity, as both groups performed at ceiling. In other cases, a perceptual deficit is observed in deaf individuals, where heightened sensitivity within the periphery occurs at a cost of lower visual performance in the central visual field (Proksch and Bavelier, 2002). These findings are consistent with the perceptual deficit hypothesis. However, it should be noted that there are also a number of studies that do not support either hypothesis (Bross, 1979; Paranis, 1983; Reynolds, 1993). Reynolds (1993) carried out a central visual detection task, where the target was displayed for 100ms, 2.2 ° from fixation. The reaction time of deaf individuals did not differ from hearing controls.

A large body of research indicates however that advantages in visual perception are specific to motion processing. There is still some variation present amongst tasks used to investigate these advantages, and behavioural differences between healthy and deaf subjects are not always observed (Bavelier et al., 2000; Stevens and Neville, 2006; Hauthal et al., 2013). In order to determine what type of motion processing is particularly heightened in

deaf subjects, e.g. localisation or discrimination, Hauthal et al. (2013) employed a task with coherently moving and static dots. These were presented in two apertures on either side of a centred fixation point at 6.25 ° eccentricity. Deaf and hearing individuals did not differ in their ability to localise movement. However, when asked to discriminate small angular differences in the direction of dot motion, the deaf participants responded faster and more accurately. Of note, this effect was not specific to the periphery, as the stimuli were presented in the perifoveal visual field only. Additionally, kinetic perimetry tests, where a subject has to detect a dot moving in from the far periphery, also demonstrate higher sensitivity in deaf individuals in the periphery (Stevens and Neville, 2006; Buckley et al., 2010).

In summary, although heightened visual abilities in deaf individuals are specific to motion processing, the current body of evidence is nevertheless conflicting. This variability may be partly accounted for by the substantial differences between experimental paradigms, a factor that is beginning to be addressed in the literature relating to sign language use and attentional load.

1.6 Effects of sensory experience

Several arguments suggest that the superior visual abilities in deaf individuals are developed due to the use of sign language as it relies highly on the processing of dynamic visual information. Using a motion direction discrimination task to dissociate the effects caused by deafness and the use of sign language, Neville and Lawson (1987) recruited hearing participants fluent in American Sign Language (ASL), alongside hearing non-signers. Apparent motion stimuli were presented within the central and peripheral visual field (18 °), whilst brain responses were recorded in the form of event related potentials (ERPs). No group differences in reaction time or ERP signals were observed within the central visual field. However, deaf subjects were faster and more accurate at responding to apparent motion presented in the periphery. ERP signals showed larger amplitudes within deaf participants during peripheral visual stimulus presentation. Amplitudes over posterior occipital cortex were larger for the hearing group, while deaf subjects instead showed higher amplitudes over regions of the anterior temporal as well as parietal cortex. This suggests a wider neural network of processing within deaf subjects. Moreover, the hearing signers

did not display any enhancements during peripheral visual field motion processing, indicating that the enhanced behavioural and physiological visual processing in deaf subjects is linked to sensory loss, and not the use of sign language.

Building on these findings, a lateralisation effect was observed by (Bosworth and Dobkins, 2002), demonstrating a right visual field advantage during a motion direction discrimination task in the deaf and hearing signers. Deaf subjects performed better within the right peripheral visual field (15.4 °) compared to the left visual field, whilst the hearing groups showed the opposite effect. The authors also reported a lower right visual quadrant advantage in deaf subjects compared to both hearing groups (signers and non-signers). Therefore, the lower right hemifield quadrant as well as peripheral visual field advantages can be attributed to hearing loss, and not the use of sign language. Alongside possible effects of sign language, prolific video game players show an extended sensitivity in the periphery when compared to hearing non-video game players, yet deaf individuals show a larger visual area of sensitivity than these two groups, apparent predominantly below the horizontal meridian of the visual field (Buckley et al., 2010). Likewise, a study by Bavelier et al. (2012) showed that video game players performed better at various behavioural tasks, including visual motion coherence judgements. Taken together these strands of evidence indicate that sensory experience and training can result in the enhancement of visual perception in hearing individuals, similar to those observed in deaf individuals, even in later stages of life.

1.7 Effects of attention

The influence of attention has also been argued to drive visual processing differences, where a growing body of evidence has begun to show that attentional effects can be linked to visual field processing advantages in deaf individuals (Bavelier et al., 2000; Proksch and Bavelier, 2002; Dye et al., 2009). For example, in a shape discrimination task, deaf participants were more distracted by incongruent shapes presented in the periphery while the hearing participants were more distracted by central stimuli (Proksch and Bavelier, 2002). However, it is not clear in this case whether the heightened sensitivity observed is a result of faster orienting of attention towards the peripheral visual field, or increased sensory input from peripheral visual field representations.

In a more recent experiment, (Bosworth et al., 2013) employed a new set of visual processing tasks to investigate the possible influence of attention. Deaf participants displayed a peripheral motion processing advantage with a right visual field bias, whilst the hearing participants did not. When comparing the conditions of either high or low attentional load, no differences were detected between the deaf and hearing groups. Therefore, the data suggest that the heightened sensitivity in the peripheral visual field is potentially independent of attentional modulation. These studies collectively demonstrate that the visual enhancements seen within early deaf individuals cannot be explained by sign language use or attentional influences alone, indicating plasticity as a result of sensory loss within the visual modality.

1.8 Neural responses to peripheral visual motion processing

Deaf individuals show superior visual abilities within motion processing (Bosworth et al., 2000; Neville and Lawson, 1987; Stevens and Neville, 2006; Buckley et al., 2010), and a number of fMRI studies have investigated neural responses of deaf and hearing individuals to motion stimuli in fMRI. There are two specific visual regions highly involved in responding to motion information, specifically motion areas V5/MT+ and V6, which should be considered as possible neural substrates of the heightened visual sensitivity in deaf individuals (Tootell et al., 1996; Huk et al., 2002; Galletti et al., 1999; Pitzalis et al., 2006).

In both humans and non-human primates, the middle temporal cortical area MT+/V5 has been identified as highly selective to processing motion (Tootell et al., 1995). This area consists of sub regions MT and MST (Huk et al., 2002). The MT region (posterior part of MT+) displays a retinotopic map of the contralateral visual field. Conversely, the MST region does not possess a clear retinotopic map, but instead displays wide array of receptive fields which are highly involved in motion processing (Tootell et al., 1996). Area V6, first identified in the macaque by Galletti et al. (1999), shows strong activation to the contralateral visual field that extends up to 80 °. Unlike other early visual cortical areas, the representations of the central visual field is not magnified relative to the periphery in V6 (Galletti et al., 1999; Pitzalis et al., 2006). V1, V2, V3, V3A, V3B, and V4 have large representations of central visual field (cortical magnification), but V6 differs by possessing

disproportionately larger peripheral representations (Pitzalis et al., 2006). In addition, V6 has larger receptive fields than earlier visual areas. V6 and V5/MT+ are outlined in Figure 1.3.

Recent studies have investigated the functional specificity of motion areas in the human brain and found that egocentric motion strongly recruits area V6, more so than any other motion area (Cardin and Smith, 2011; Pitzalis et al., 2013; Billington et al., 2013). Pitzalis et al. (2013) further suggest that area V6 is involved in distinguishing object motion from self-motion by providing information that differentiates moving and static objects during egocentric motion. The neuroanatomical evidence to date therefore provides a platform for relating the functional specificity of brain areas V5/MT+ and V6 to the observed behavioural enhancements within the processing of peripheral motion in deaf individuals.

A recent study further highlights the importance of these motion areas. The extent of the peripheral visual field investigated was expanded to +/- 90 ° by Buckley et al. (2010) who found significant differences in visual field sensitivity between deaf and hearing participants as measured through Goldmann kinetic perimetry. This task requires participants to detect a visual stimulus moving towards fixation, whilst their head is placed in a dome encapsulating 90 ° of their visual field. The effects were found in both the near-peripheral (around 30 °) and far-peripheral (around 60 °) visual field, with deaf participants demonstrating a larger area of sensitivity in both visual field regions. The extent of this heightened sensitivity points to the specialised involvement of far-peripheral motion processing areas, possibly V5/MT+ or the more recently discovered area V6, which has a disproportionately larger peripheral bias in comparison to earlier visual areas (Pitzalis et al., 2013).

Bavelier and colleagues (Bavelier et al., 2000, 2010) examined visual responses of deaf and hearing participants using fMRI. Random dot motion was presented in the central and near-peripheral visual fields. This study also controlled for sign language, with a hearing native signing group recruited alongside a hearing non-signing control group. Participants were instructed to attend to either brightness or velocity changes within either the central (0.4-1.73 °), near-peripheral (6.66-8 °) or whole visual field (0.4-8 °). When attending to the motion stimulus the three groups demonstrated similar activation patterns in the central and whole visual field conditions. Importantly, however, deaf subjects showed a larger extent of activation within area MT+/V5 during the peripheral condition than hearing

signers and non-signers. Collectively the above findings show us that deaf individuals exhibit an advantage in motion processing within the periphery, and that this difference cannot be attributed to the use of sign language.

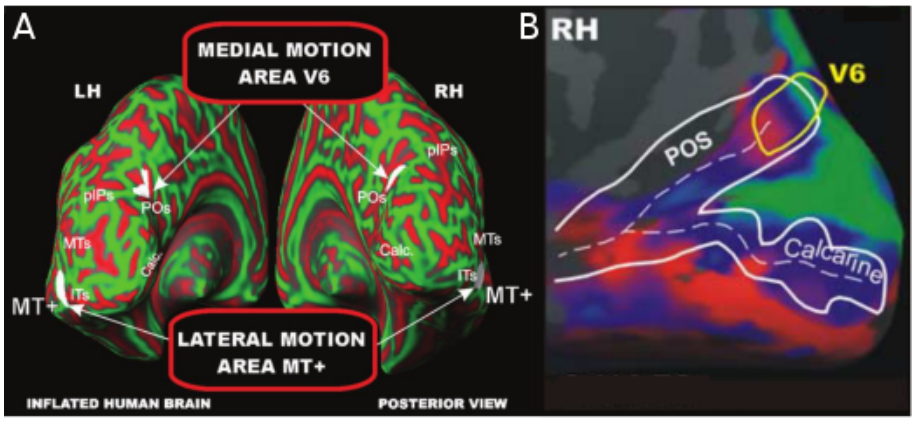

Figure 1.3 – A) Brain location of the two motion areas V6 and V5/MT+ displayed on a left and right inflated hemispheres (posterior view) Source: Pitzalis et al., 2010. B) Representation of retinotopic maps of eccentricity, extending to 50° on a flattened cortical map of an example participant. Source: Pitzalis et al. (2006)

1.9 Cross-modal effects

In a parallel line of evidence, animal studies have demonstrated that a deprived auditory cortex can be recruited to achieve enhanced visual processing in congenital deafness. For example, superior performance in deaf cats to peripheral visual localization is mediated by cross-modal effects seen in the auditory cortex (Lomber et al., 2010). Here, visual tasks involving target localisation or motion detection were administered to deaf cats whilst the selective application of cooling loops was used to de-activate specific regions of their auditory cortex. When the posterior auditory cortex of deaf cats was deactivated, the advantage over hearing cats in the task was nullified, with the same pattern of results emerging when the dorsal auditory cortex was deactivated during the motion detection task. Both results show the causal link between neural substrates within the sensory deprived auditory cortex and the heightened visual abilities in deaf cortex. However, it is not ethically viable to introduce such measures in human cortex, emphasising the importance of other measures such as fMRI in isolating the critical neural substrates of heightened visual performance.

Cross-modal recruitment of the auditory cortex is also observed in humans when performing tasks involving visual motion (Fine et al., 2005; Armstrong et al., 2002; Bottari et al., 2014). To this end, Fine et al. (2005) investigated visual responses of early deaf signers, hearing signers, and non-signers to a dot motion stimulus 15 ° in the periphery on either side of a central fixation point. When observing motion attention was also manipulated with participants required to either detect luminance changes of the fixation point or just passively observe motion. The study did not find any effects of attention upon visual motion processing across all groups of participants however, unlike the hearing participants, deaf individuals did recruit the auditory cortex in the visual processing of motion.

These interesting findings have been bolstered by recent fMRI investigations, namely Scott et al. (2014), who conducted an fMRI experiment aiming to record differences in brain responses within the auditory cortex (Heschl's gyrus) and whole brain between deaf and hearing participants. In this case, visual stimulation occurred in either perifoveal (2-7 °) or peripheral (11-15 °) visual fields. Deaf participants showed higher responses in auditory cortex within the peripheral condition over perifoveal presentation, which was not observed in hearing participants. Moreover, in the whole brain analysis, greater activity was found in the deaf individuals across the primary auditory and visual cortex, MT+/V5, superior-temporal and the posterior parietal cortex, suggestive of widespread neuroplasticity.

The studies outlined above indicate that sensory deprivation can cause cortical reorganization. However, structural and functional changes observed in the superior temporal sulcus in deaf individuals may be influenced not only by sensory but also cognitive aspects. In deaf individuals, language development relies on visual communication such as sign language and lip-reading. In an fMRI study, Cardin et al. (2013) investigated the effects of life-long sign language use in hearing and deaf individuals. The additional novelty of this research was the inclusion of deaf non-signers. As deaf signers rely on oral speech reading, the study aimed to disentangle plastic changes caused by life-long sign language use and life-long auditory deprivation. Based on their results, they concluded that plasticity observed in the left superior temporal cortex originated from language experience, and right superior temporal cortical plasticity was associated with sensory deprivation. Furthermore, at lower BOLD signal thresholds, deaf participants demonstrated greater activation in area MT+ and in the planum temporale. The study by Cardin et al. (2013) was therefore uniquely able to disentangle effects of deafness and the modality through

which a language is learned. This process appears to be significantly different from that experienced by early deaf signers. Namely, this research shows that higher cognitive areas process sign language, and the effects of sign-language and its acquisition would not be reflected in primary or higher visual areas. In sum, the evidence thus far indicates a wide selection of neural areas are recruited in cross-modal plasticity as a result of early auditory loss.

1.10 The auditory cortex

The auditory cortex is mainly defined by areas receiving thalamic inputs from the medial geniculate complex (MGC), although the specific locus of the auditory cortex in humans is not as well defined, as visual regions for example, given that the specific MGC projections are not known (Hackett, 2011). As the definition of auditory cortex in humans cannot reply on these projections, it is instead mainly defined on the basis of its neuronal architecture and neurochemistry, which in turn has formed the basis of a number of exploratory neuroimaging and electrophysiological studies. The human auditory cortex occupies the posterior area of the superior temporal cortex including Heschl's gyrus, the planum temporale and a portion of the posterior superior temporal gyrus. As previously discussed, the auditory cortex in deaf individuals is reorganised to process the remaining visual (Finney, 2001; Lomber et al., 2010; Karns et al., 2012) and somatosensory inputs (Karns et al., 2012). Accordingly, there are a number of different subregions within the wide scope of auditory cortex, including the planum temporale, primary auditory cortex (Heschl's gyrus) and secondary auditory regions such as the posterior superior temporal sulcus (pSTS), all of which have previously been investigated in line with cortical plasticity in deaf individuals (Sadato et al., 2005; Fine et al., 2005; Karns et al., 2012; Scott et al., 2014).

While the auditory cortex is quite a large region, depending on the subregion included, it can nevertheless show a differential involvement in motion processing in deaf individuals. Importantly, no previous study to date has implemented wide-field optic flow motion stimulation within three separate regions, including primary auditory cortex as well as regions posterior and anterior to it within the temporal cortex, within this population. A number of higher cognitive areas and the recruitment of auditory cortex have been implicated as

possible substrates of cortical plasticity in auditory deprivation. However, an emerging body of evidence indicates that the observed visuo-spatial behavioural advantages in early deaf individuals could be linked to intramodal plasticity within the visual system, apart from those seen in the auditory cortices or higher cognitive areas. For example, enhanced electro-physiological activity in primary and secondary visual cortex have been shown to correlate with a more rapid detection of abrupt visual stimuli by deaf individuals. In this case, the behavioural enhancement did not show any involvements of auditory cortex (Bottari et al., 2011). Smittenaar et al. (2016) have shown thinner gray matter thickness in the primary visual cortex of deaf individuals, when compared to hearing controls, but this measure did not relate to behavioural visual advantages of the study. A more recent study however, found correlations between structural measures of the planum temporale (secondary auditory cortex) with visual task performance in deaf individuals (Shiell and Zatorre, 2016). It is therefore not fully clear how plasticity in the shape of structural differences can facilitate behavioural advantages in deaf individuals.

1.11 Conclusions

Important questions still remain unanswered concerning possible intramodal plasticity in deaf individuals. Recently, far-peripheral visual sensitivity was found to be correlated with differences apparent between deaf and hearing individuals in the structure of the retina (Codina et al., 2011b). The deaf individuals demonstrated a larger neuroretinal rim area, thought to reflect a larger number of retinal ganglion cells. Moreover, the retinal nerve fibre layer (RNFL) within the peripapillary region was significantly thicker in deaf participants, particularly in projections from the temporal retina, which processes peripheral vision (Codina et al., 2011b). The thicker RNFL result correlated directly with behavioural measures of peripheral visual field sensitivity (Goldmann kinetic perimetry), linking the behavioural advantages to structural differences observed. This data suggests plasticity at stages earlier than primary visual cortex (Codina et al., 2011b). We aim to reveal effects of the structural differences in the retina of the primary visual cortex in the context of heightened far-peripheral sensitivity in deaf adults. Neural substrates involved in far-peripheral visual processing are challenging to identify with fMRI and methodological constraints make it difficult to stimulate the far-peripheral visual field reliably. As a result, the neural substrates tied to the effects of retinal plasticity have not

been widely investigated thus far.

1.12 Summary

In summary, there is substantial evidence to support the effect of profound and congenital auditory loss upon peripheral visual processing. This translates into behavioural differences where deaf adults show faster reaction times and greater sensitivity in the peripheral visual field, especially in motion processing. The influences of sign language use (Neville and Lawson, 1987; Bosworth and Dobkins, 2002), and attention (Bosworth et al., 2013) were experimentally ruled out as influences upon plasticity within primary visual cortex. Deaf individuals also display a greater involvement of motion areas, MT+/V5 (Bavelier et al., 2000) and the re-organisation of the sensory cortices, such as the primary auditory cortex (Finney, 2001; Scott et al., 2014). Effects in auditory regions have so far incorporated motion stimulation in limited eccentricities, and only in selected subregions of auditory cortex. This study will therefore investigate responses to far-peripheral optic flow motion in deaf and hearing individuals, within a larger scope of regions anterior and posterior of primary auditory cortex. There is also evidence to support early structural changes in the visual system of congenitally deaf individuals. The retinal nerve fibre layer is thicker in deaf participants, compared to hearing individuals, which correlates with the enhancement of peripheral visual field sensitivity (Codina et al., 2011b). If differences can be observed as early as the retina, this may influence cortical plasticity as early as the primary visual cortex. These differences between the enhanced visual processing and retinal structure should be apparent at much further eccentricities than those studied to date using fMRI. An appropriate avenue for subsequent investigations should exploit intramodal observations to identify the potential, and specific, cortical regions that mediate the perceptual enhancement seen in the far-peripheral visual field.

Chapter 2

Methods

2.1 Overview

This chapter provides an overview of the methodological approaches used in this thesis. The methods used include a combination of data in form of functional and structural MRI, as well as psychophysical measures. The aim was to investigate brain plasticity in relation to visual processing advantages observed amongst deaf individuals. This was investigated by quantifying cortical plasticity in the form of structural and functional measures in early visual areas V1, V2 and V3 in the brains of deaf and hearing participants. A novel methodological approach developed for fMRI for this body of work allowed us to stimulate the far-periphery of these visual areas, stimulating a total of 144 ° of the visual field along the horizontal meridian. Secondly, the aim of the study was to examine neural responses in motion selective regions, and how differences here correlate with motion perception. The study used the wide field fMRI stimulus presentation set up to present participants with far-peripheral visual motion to target cortical areas processing motion, which possibly underlie visual motion processing advantages in deaf individuals. This study included definitions of visual motion areas V5/MT+ and V6. Auditory regions were also investigated, as previous studies show large cross-modal plasticity within auditory cortex of deaf individuals, but effects in far-peripheral motion processing of this area are still largely unknown.

2.2 Participants

All participants self reported normal or corrected to normal visual acuity and had no known neurological conditions. Informed written consent for scanning and behavioural components of the study were given by each participant in accordance with the Declaration of Helsinki. The study was approved by The York Neuroimaging Centre Research Governance Committee (Department of Psychology, University of York).

2.2.1 Deaf Subjects

The described experiments included 16 deaf participants, with a mean age of 34.1 (five females, median 34.6, range 20-48). Three male and one female subject were left handed. All participants self reported the extent of their hearing loss. Out of the group, three participants were severely binaurally deaf (>61db) and the remaining 13 were profoundly (>81db) binaurally deaf (WHO, 2016; see Table 2.1 for more details). They were recruited through advertisements at the University of York, as well as through invitations extended through collaborators, Dr Charlotte Codina and Dr David Buckley from Sheffield University. As an incentive, deaf subjects were paid for participating and reimbursed for their travel expenses, if travelling from outside of York. Our deaf cohort consisted of individuals who had been deaf from birth or an early age. A key difference between hearing and deaf individuals is the use of a visuo-spatial language. Sign language use has been investigated as a factor influencing behavioural differences seen in deaf individuals (see section 1.6). Our deaf group had varying levels of exposure to BSL and English (see Table 2.1). Not all participants knew the cause of their deafness, however the study did ensure that participants do not suffer from Ushers syndrome, which often leads to a combined early-onset visual and auditory impairments (Brennan and Bally, 2007). As outlined previously (see section 1.6), it is important to consider other factors that can influence cross-modal plasticity and differences in cortical processing. The heterogeneity of the sensory impairment, as well as exposure to sign language and use of hearing aids within the deaf population studied needs to be considered when interpreting experimental results. Based on previous literature extracting any effects, other than deafness, which influence plasticity in this population, the study reports, with confidence, investigations which target behavioural and neural effects of plasticity caused specifically by auditory deprivation.

Table 2.1 – Characteristics of adult deaf participants

Subject Number	Age (at testing)	Gender	Handedness	1st Language	BSL?	Cause of Deafness	Age of Onset (years)
1	43	M	Right	English	Yes	Hereditary	Birth
2	48	M	Left	BSL	Yes	In utero measles	Birth
3	47	M	Right	English	Yes	Hereditary	Birth
4	46	M	Right	English	Yes	Rubella	Birth
5	40	M	Right	English	Yes	Sensorineural loss	Birth
6	20	F	Right	English	No	Unknown	2-4 yo
7	20	F	Left	English	Yes	Unknown	Unknown
8	48	F	Right	English	Yes	Unknown	Unknown
9	23	F	Right	English	Yes	Sensorineural loss	Birth
10	31	M	Left	BSL	Yes	Hereditary	Birth
11	31	M	Right	English	Yes	Unknown	Birth
12	33	F	Left	BSL	Yes	Unknown	Unknown
13	39	M	Right	BSL	Yes	In utero measles	Birth
14	20	M	Right	BSL	Yes	Hereditary	Birth
15	37	M	Right	English	No	Birth defect	Birth
16	20	M	Left	English	No	Unknown	Birth

2.2.2 Hearing Subjects

A total of 30 hearing participants with a mean age of 27.2 (13 females, median 25.5, range 20-48) took part in the outlined experiments. Three males and one female participant were left handed. One of our hearing subjects had basic BSL knowledge, acquired only during the 2 years prior to taking part in this study. This group of participants was recruited through invitation and advertisement at The University of York.

2.3 Imaging Parameters

All functional and structural MRI data were acquired with a GE Healthcare 3 Tesla Sigma HD Excite scanner with a 16 Channel Posterior Brain Array coil (Nova Medical) at The York Neuroimaging Centre (YNiC). The 16-channel coil was used as it provides higher MR sensitivity to signals in the occipital cortex and improves the signal-to-noise ratio.

2.3.1 Structural Data

The structural data were acquired with a high resolution T1-weighted isotropic scan sequence (TR, 8 ms; TE, 3 ms; flip angle, 12 °; matrix size, 256x256; FOV, 256mm; 176 slices; slice thickness, 1mm; voxel size, 1x1mm ^{3}). The 16 channel half-head coil, together

with the isotropic voxel resolution provide a good structural contrast, aiding the automatic anatomical segmentation of grey and white brain matter. An inplane structural proton density scan (TR, 2.7s; TE, 36ms; flip angle, 90 °; matrix size, 512x512; FOV, 192mm; 39 slices; slice thickness, 2mm; voxel size, 0.37x0.37mm ^{3}) was acquired prior to each functional sessions stimulating each hemifield in order to aid the co-registration of functional data with structural data, as the sequence provides a high resolution volume in the same slice prescription as the functional data. A T2* gradient echo scan (TR, 400ms; TE, 4.3ms; flip angle, 25 °; matrix, 256x256; FOV, 260mm; 88 slices; slice thickness, 2mm; voxel size=1.015x1.015x2mm ^{2}) was acquired with the same slice prescription as the inplane structural for a subset of participants (3 hearing, 4 deaf) as it was introduced later in the protocol. The scan aids the further correction for spatial inhomogeneities in structural scans, due to frontal signal drop off (see Figure 2.1) introduced by the posterior half-head16-channel coil (Figure 2.3).

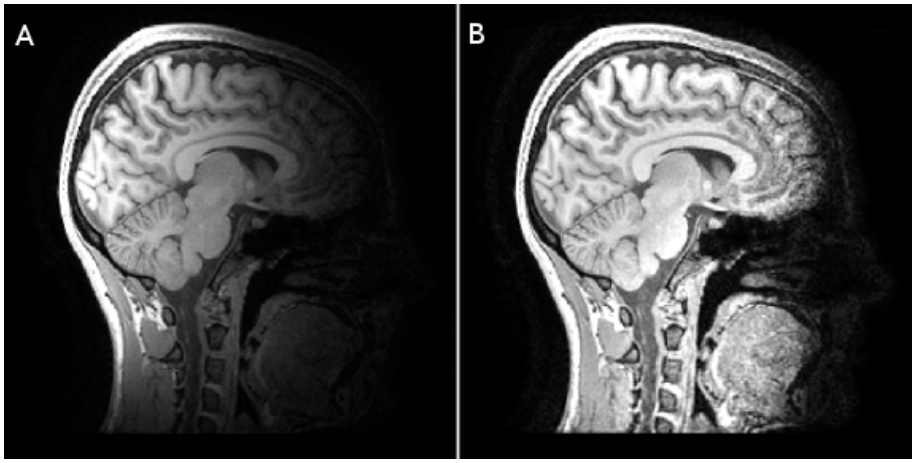

Figure 2.1 – Example of an uncorrected (A) and fast corrected (B) T1-weighted structural isotropic image acquired with a 16 channel half-head posterior array coil. The image demonstrates the signal loss drop off towards the frontal cortex.

2.3.2 fMRI Data

Functional data were acquired with a BOLD T2* EPI sequence (TR, 3s; TE, 30ms; flip angle 90 °; matrix size, 128x128; FOV, 192mm; 39 slices; slice thickness, 2mm; voxel size, 1.5x1.5mm ^{3}. The first three functional volumes were discarded to allow the scanner to reach a stable magnetisation level. The slice prescription (see Figure 2.2) was selected to cover the occipital pole, as our focus was on early visual areas V1, V2 and V3, and

motion areas, including area V5/MT+ which is located in the ascending limb of the lateral occipital sulcus (ALTIS, specified in Dumoulin et al., 2000) as well as the parieto-occipital sulcus, at the top of which V6 is located (Pitzalis et al., 2006). The 16-channel coil provides higher MR sensitivity to signals in the occipital cortex and combined with the 1.5x1.5 mm voxel sampling in these functional images improve the signal-to-noise ratio, as tested at YNiC by Silson (2013, Thesis reference, section 3.5.3).

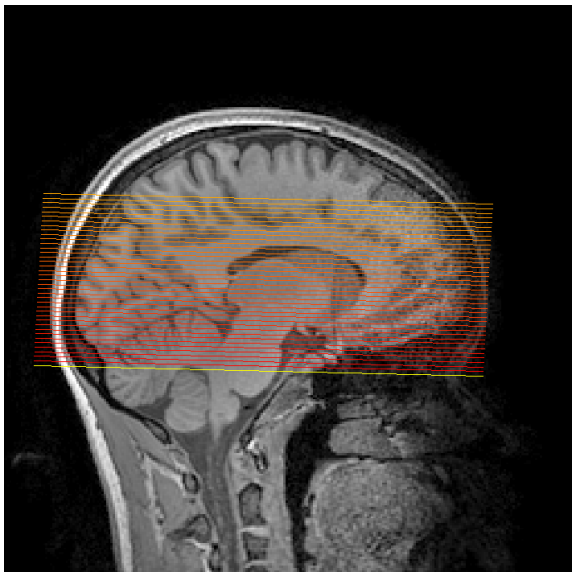

Figure 2.2 – A slice prescription example from a functional scan. The slices are positioned just under the occipital pole and angled in order to also include the top of the parieto-occipital sulcus (POS) where V6 resides. This structural scan has been corrected for magnetic field inhomogeneities.

2.4 Visual Stimulus Delivery in fMRI

Visual stimuli were generated using Psykinematix 1.4 (Beaudot, 2009) on a Mac mini OS X and projected to participants through the scanner bore with use of a projector (Dukane 8942 ImagePro / PROPixx DLP LED). The participants viewed the stimuli through a wide mirror, mounted on the head coil, allowing them to see the projection on a custom in-bore acrylic screen (3050mm x 2030mm) mounted behind the head coil (see Figure 2.3). The stimuli were viewed lying supine, at a distance of 275 mm. For the Dukane projector, the average luminance of the display was 97.87 cd/m^2 measured with a Minolta Luminance Meter (LS -100/LS 110) and mean luminance of 98.6 cd/m^2 (min:max

luminance 2.42:199.7 cd/m^2) for the proPIXX projector, measured with a Spyder 3 Pro calibration device, which is compatible with the Psykinematix stimulus delivery software. The head of each subject was stabilised with foam pads placed around the participants head inside the head coil and a forehead velcro-strap to reduce motion artefacts. The study delivered stimulus to each hemifield in separate functional scans to retrieve signals from the far-periphery, extending 72° into the visual field along the horizontal meridian. All scans used passive viewing and continuous fixation throughout the session. Depending on the stimulus used, the fixation cross was either a grey '+' sign, 0.87° in size (for retinotopy), or a red '+' sign, 0.6° in size (for optic flow) and was located 36° off the display centre, on the horizontal meridian, to map the given hemifield. In order to prevent a gradual movement of the head towards the fixation cross, the head was tilted slightly (ca. 3°) towards the fixation cross in the given hemifield tested. The first data collected indicated a gradual movement towards fixation, prompting us to tilt participants heads to minimise motion confounds introduced by this gradual shift. All apart from a subset of hearing (four) and deaf (five) participants had their heads tilted.

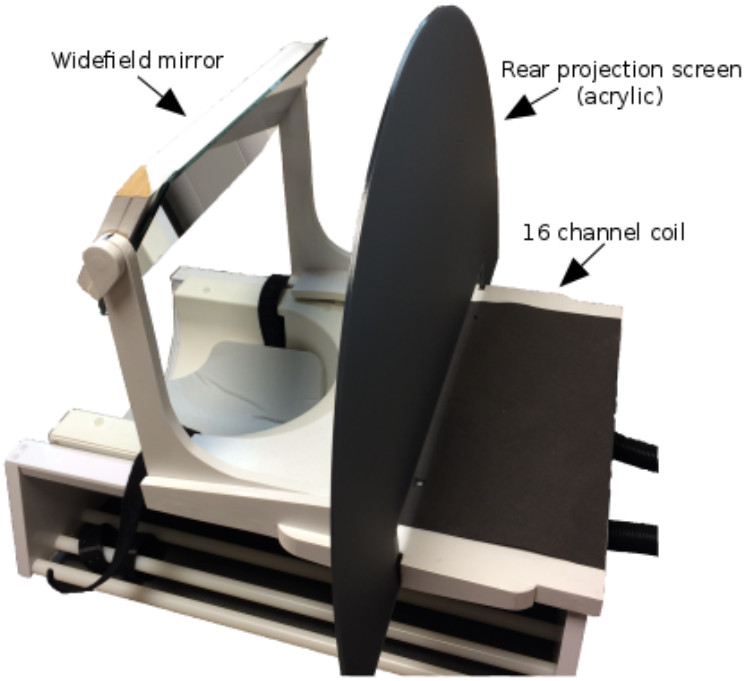

Figure 2.3 – A photograph of the MRI data acquisition set up. A custom made acrylic screen and wide angle mirror are slotted on the 16 channel Nova Medical half-head posterior coil.

Instructions were communicated in the MRI scanner between scans, verbally to hearing participants and visually via PowerPoint slides to deaf participants. The deaf participants

were asked to push down a button when a message appeared on the screen, and release it when they had read the message and were happy to proceed, whilst hearing subjects responded verbally. Every participant was provided with an emergency buzzer, which could be pressed at any instance, if they wished to quit the scanning procedure. Presenting stimuli in the far-peripheral visual field within fMRI is met with practical constraints, for example, the bore size limits the possible screen size which can be used for stimulus delivery. To our knowledge, this study was able to map the periphery to the furthest known extent (72 °). However, other labs have employed wide field stimuli, extending out to 55 ° (Pitzalis et al., 2006) and 60 °, with the use of magnifying lenses (Wu et al., 2013, Yan et al., 2009).

2.5 Retinotopic Mapping of Visual Areas

To identify and measure visual field maps in the brain, phase encoded retinotopic mapping procedures were used in fMRI (DeYoe et al., 1996; Sereno et al., 1995; Engel et al., 1997) designed and presented on a Mac mini OS X with Psykinematix software (Beaudot, 2009). The stimuli included a rotating wedge and expanding ring (Figure 2.4) which map the cortical representation of polar angle (degrees of visual angle from the contralateral horizontal meridian, 0 °-180 °) as well as the eccentricity (distance from the centre of gaze, 0 °-72 °). The BOLD activation values are correlated with a reference function derived from the time course of the retinotopic stimulus presentation. fMRI responses are quantified as the phase and amplitude of the sinusoid that best fit the average time series of voxel response within the visual cortex (as described in 1.3). The retinotopic stimuli were modified to a wide field presentation, mapping each hemifield representation in separate scans in turn, to the extent of 72 °, encapsulating 144 ° of the visual field, along the horizontal meridian, (Figure 2.4 A,B). This approach is crucial to our study, as it allows us to investigate the visual representation of the far-periphery in visual cortex, which to our knowledge, is the furthest fMRI visual field mapping to have been carried out in human visual cortex.
Within this body of work, two variations of retinotopic stimuli were used. The first version was carried out during pilot scanning of five deaf and four hearing participants. The following 11 deaf participants and 16 hearing controls were scanned with a second version of retinotopic stimulus the parameters of both versions were very closely matched. The retinotopic stimuli used for pilot scanning were generated with MatLab (version R2012a;

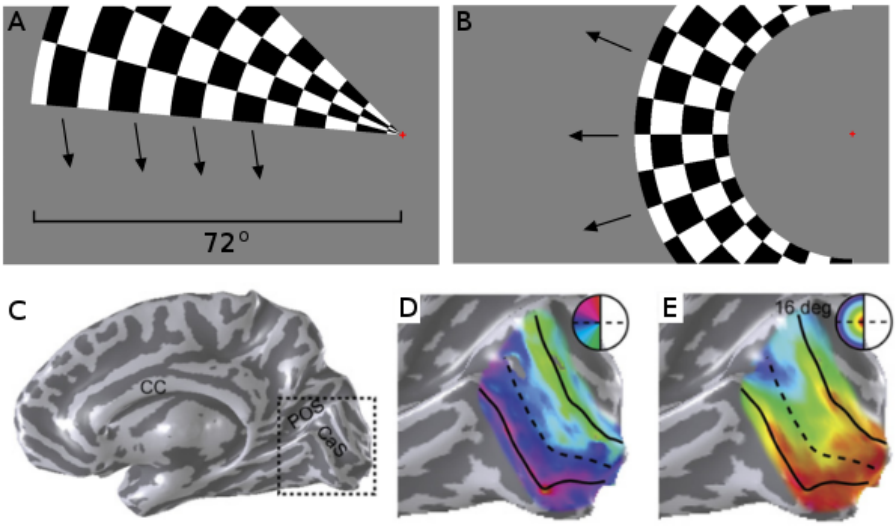

Figure 2.4 – Example frames of wedge (A) and ring (B) retinotopic stimulus (version two) used in the current experiment to activate the left hemifield. Each hemifield was tested separately, with the fixation cross placed 36 °on either the left or right side of the screen. All stimulus counterphase-flickered at 4 Hz and extended from fixation to 72 ° of visual field angle. The arrows indicate the sequential direction in which the checkerboard pattern moved. An example inflated right hemisphere (C) is labelled with the CC- corpus callosum, POS- the parietal-occipital sulcus and CaS- the calcarine sulcus. Figures D and E represent a close up of CaS, where V1 resides, with a colour map overlay which are coded according to the response phase at each visual field location for polar angle (D) corresponding to the rotating wedge (A) and eccentricity (E) elicited by the expanding ring stimulus (B). Images (C), (D) and (E) are from Wandell et al. (2007).

The MathWorks, Natick, MA) and presented with matVis (Neurometrics Institute). These included wedge and ring stimuli and both they contained high contrast reversing checker boards, flickering at a rate of 6 Hz (100% luminance contrast, 50% luminance background, see Figure 2.4, A,B). The rotating wedge stimulus extended horizontally to 72 °, vertically ca. 20 °, covered 30 ° of the visual field and stepped in 11.25 ° increments, beginning at the upper vertical meridian within both hemifield conditions. The expanding annulus had a total annular width of 30 °, three ring-segments of sixteen wedges. As the rings approached the edge of the stimulated field, each ring was replaced by a new one originating from the centre of fixation. A fixation cross, a grey '+' sign, 0.87 ° in size was present throughout the entire scan. The second version of retinotopic stimuli following the pilot scan also contained wedge and ring stimuli, consisting of high contrast reversing checker boards, flickering at a rate of 4 Hz (100% luminance contrast, 50% luminance background, see Figure 2.4 A,B). The rotating wedge stimulus also extended horizontally to 72 °, vertically ca. 20 °, containing four segments covering 30 ° of the visual field and stepped in 15 ° increments, beginning at the upper vertical meridian for the right hemifield, and at the lower vertical meridian in the left hemifield. The expanding annulus was comprised of three ring-segments of eighteen wedges, with a total annular width of 30 °. As the rings approached the edge of the stimulated field, each ring was replaced by a new one originating from the centre of fixation. A fixation cross, a red '+' sign, 0.6 ° in size, was present throughout the entire scan. Both retinotopic scans comprised of cycles lasting 36 seconds, of twelve motion steps, with eight full repetitions. The motion steps contained a wrap-around effect to ensure a good fit between the BOLD response and sinusoidal nature of the retinotopic data. The order of retinotopic scans and hemifield was counterbalanced within each group to avoid systematic variations in response across stimulus types, as fatigue can increase in participants over time when being scanned, and can affect the quality of the signal within each functional scan.

2.6 Data Preprocessing

2.6.1 Preprocessing of Anatomical Data

T1-weighted images were corrected for magnetic spatial inhomogeneities with FMRIBs Automated Segmentation Tool (Zhang et al., 2001, (FAST;). A subset of participants also

had a T2* gradient echo scan acquired, which is divided by the T1 structural image (FSL maths), further aiding the aforementioned FAST correction (see Figure 2.1). These data were processed with the FreeSurfer 5.3 analysis suite (http://surfer.nmr.mgh.harvard.edu/). The script used (autorecon) reconstructs the grey and white matter surface (Dale et al., 1999). The occipital lobe of the reconstructed image was then corrected by manually segmenting and topology checking in ITK-Snap (Yushkevich et al., 2005, version 2.2.0, http://www.itksnap.org/pmwiki/pmwiki.php). These segmentations were used to create flattened cortical representations (Dougherty et al., 2003; Wandell et al., 2000) on which the retinotopic data were displayed using the mrVista toolbox (Wandell et al., 2000) written for MatLab (version R2012a; The MathWorks, Natick, MA) .

2.6.2 Preprocessing of Retinotopic Data

Phase encoded retinotopic scans were processed with the mrVista toolbox (version 3, run on Matlab 7.14; Wandell et al. (2000). In order to correct for motion, the T2* functional volumes were aligned to the first acquired volume of the session. Data was slice time corrected and high-pass filtered to remove baseline drifts. MrVista corrects for motion within and between functional volumes and uses a mutual information motion correction algorithm (Nestares and Heeger, 2000). The corrected functional scans were co-registered to the coordinate space of the high resolution structural image for each participant using FMRIBs Linear Image Registration Tool (FLIRT; Jenkinson et al., 2001) and the Nestares alignment code (Nestares and Heeger, 2000) which is part of the mrVista toolbox. To aid data visualisation, the phase encoded retinotopic data was displayed on a flattened representation of the occipital cortex (Dougherty et al., 2003; Wandell et al., 2000). The flat maps provide an easy way to identify visual areas (described in Section 2.7). The flattening process however distorts the distance and area measurements within the 2D dimensions, all coordinates defined were therefore transformed into the 3D cortical manifold and measurements extracted thereafter (Dougherty et al., 2003). Visual areas V1, V2 and V3 were defined on the flattened representations.

2.7 Delineation of Visual Areas

The delineation of visual field maps in visual cortex was based on previous literature, which established the identifying features of visual areas (Engel et al., 1997; Sereno et al., 1995; DeYoe et al., 1996; Wandell et al., 2007). As such, V1 and the ventral and dorsal representations of V2 and V3 were functionally defined based on the phase of the responses of voxels to the polar angle scan. The rotating wedge stimulus travelled from the upper to lower vertical meridian in the right hemifield, and lower to upper vertical meridian in the left hemifield. The data were restricted to voxels with at least a 0.2 coherence threshold (>20% variance explained). The identifying features used to guide the delineation of visual areas were:

- The eccentricity scan providing a reliable localisation of the foveal confluence,
- A smooth progression of phases across each visual area in accordance with the known topographic representation on the cortical surface,
- The polar angle stimuli showing phase reversals, where visual areas share boundaries.

As mentioned (see section 1.2), V2 and V3 are split into upper and lower quadrant representations, which surround the full hemifield representation of V1. The data from ventral and dorsal representations of V2 and V3 were combined, after which data from areas were combined across hemispheres.

2.8 Sub-ROI, Surface, Volume and Thickness Measures

One of the main aims was to investigate differences between our deaf and hearing participants in the distribution of visual cortex relative to the visual field eccentricity it represents. To look at this, the amount of cortex dedicated to processing given eccentricity sections of the visual field were quantified within V1, V2 and V3. The subdivisions within each visual area were defined by eccentricity bins which would provide an approximately equal number of voxels in each, in order to make these comparable between groups. These bins corresponded to the representations of central (0-15 °), mid-peripheral (15-39 °) and

far-peripheral visual field (39-72 °). The sub-ROIs delineations were guided by the eccentricity data (expanding ring). Data representing the given response phase corresponding to the given extent of the visual field stimulated was displayed on the flattened cortex. This guided the manual selection of cortical surface devoted to representing the given representation, and the definition included all voxels, and was no restricted to the inclusion of only active voxels. The cortical volume (mm^3), surface area (mm^2) and grey matter

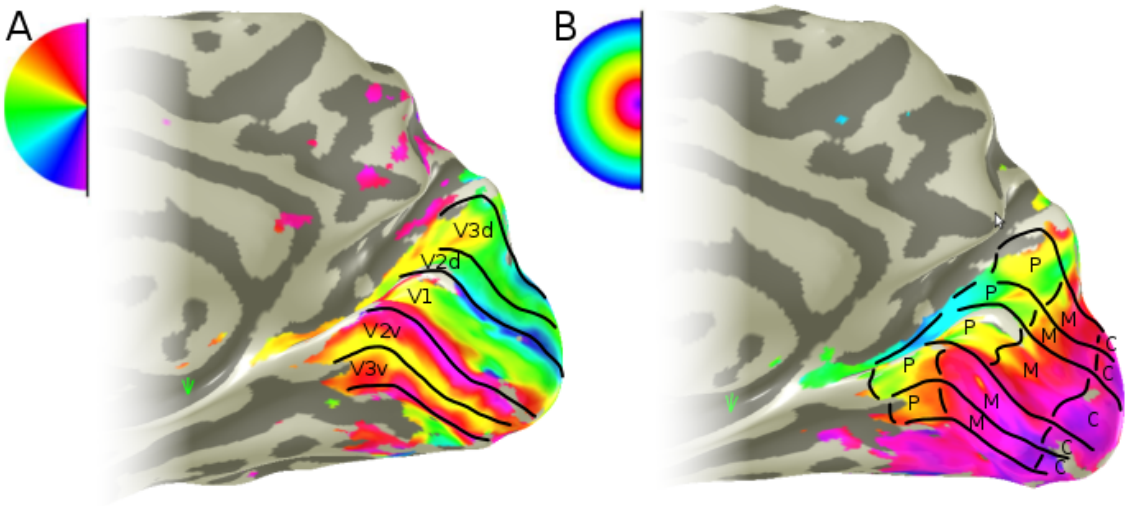

Figure 2.5 – An inflated view of the right hemispheric occipital cortex with overlaid retinoropic data. (A) shows polar angle data overlaid, on top of which definitions of V1, dorsal and ventral V2 and V3. (B) shows sub divisions within these visual areas are defined based on the expanding ring data, with the following representations of the visual field: C- represents the Central (0 °-15 °), M- mid-peripheral (15 °-39 °) and P- far-peripheral (39 °-72 °).

thickness (mm) were extracted for each sub-ROI, within each visual area (Figure 2.5). The surface area measurements were made on the 3D cortical manifold, following the method used in Dougherty et al. (2003). In this method, the visual areas are outlined on a 2D flat map, then transformed into the 3D manifold. The surface area was calculated by taking the coordinates belonging to the selected ROI and finding the nearest node on the 3D manifold describing the boundary of grey and white matter. The nodes of the ROI create the vertices of the set of triangles which form the patch on the mesh which correspond to the ROI. The sum of area of each triangle summed gives us the surface measure of the area at hand. The cortical volume measure was extracted by counting all voxels within the ROI transformed into the high resolution 3D view in mrVista ('Xform' function in mrVista).

As the voxels are $1mm^3$ isotropic, the measure gave the volume in cubic millilitres within each ROI. Mean cortical thickness was calculated by extracting the mean number of grey matter layers within each ROI, as our scans have an isotropic resolution of $1mm^3$, each grey matter layer is 1mm. The means were extracted for every visual area as well as the subdivisions within each.

2.9 Cortical Magnification

As one of the main aims was to measure the change in cortical sampling relative to the visual field, the areal cortical magnification factor was calculated in visual areas V1, V2 and V3 in each participant. This was done by dividing the cortical surface area for each ROI by the area of visual field (mm^2/$degrees^2$). This measure which is not been used in previous studies, provides an estimated surface based cortical magnification. It provides a continuous variable within each visual area, as the subdivisions are not independent. These values were log transformed ($\log(mm^2/degrees^2)$) as cortical magnification functions follow an inverse exponential, and the points were fitted with a linear regression. The gradient fitted through the three points within each visual area, V1, V2 and V3 were extracted from each participant (see Figure 2.6). The group means were extracted and compared. This provided a sampling rate within each of the three regions, which, when compared across individuals are not influenced by individuals differences in visual area size (Andrews et al., 1997; Dougherty et al., 2003). All the measures described were statistically tested within statistical software (IBM SPSS Statistics 20).

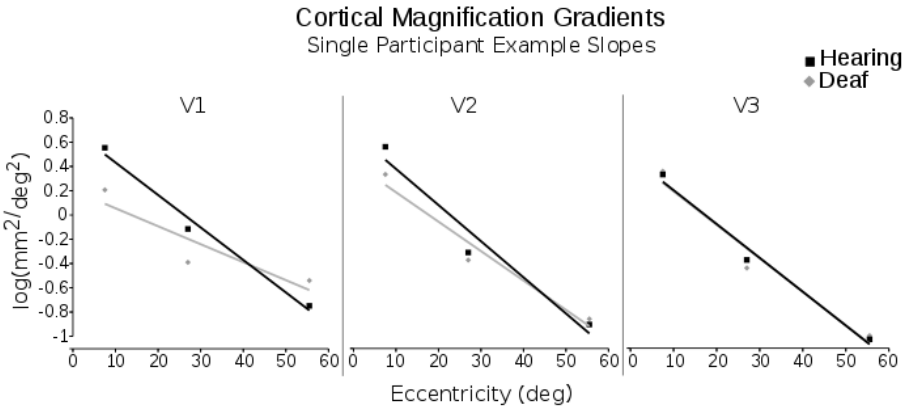

Figure 2.6 – Examples of cortical magnification gradients plotted per visual area (V1, V2 and V3) of one single hearing (black) and deaf (grey) participant.

2.10 Visual Motion Stimulus Design

Investigations of motion processing described in Chapter 4, made use of stimuli aimed to maximally activate areas V5/MT+ and V6, and consisted of a block design with high contrast optic flow field stimuli, adapted from Pitzalis et al. (2010). In the coherent motion block, motion types presented alternated between radial motion (expanding/contracting) or angular motion (clockwise/counter clockwise, see Figure 2.7). The motion presented updated every 500ms, in a random order. Dots immediately began to move along the radii to give the impression of motion expansion or contraction, to match the observer-centred impression of forward or backwards movement along their line of sight, i.e., ego-centric optic flow in depth. Angular motion followed the clockwise or counter-clockwise trajectory. The random motion condition comprised of scrambled motion with a new presentation also updated every 500ms. The central dots within all motion types moved slower than the ones in the periphery as the dot size (between 0.75 ° - 3.2 °) and speed (between 8 °/s - 64 °/s) increased in a logarithmic fashion in relation to eccentricity. In the coherent radial motion blocks this simulated motion in depth (optic flow motion generated by moving forwards or backwards). A fixation cross, a red '+' sign, 0.6 ° in size, was present throughout the entire sequence. Each cycle was 36 seconds long and consisted of a 9 second block of coherent and incoherent motion each followed by a 9 second black display with the fixation cross present (Figure 3). As with the retinotopic mapping scans, our subjects had their heads tilted slightly (ca. 3 °) towards the fixation cross in the given hemifield. All apart from four hearing and three deaf participants did not have their heads tilted during the optic flow presentation. Comparing the BOLD activation between the two motion blocks and blank periods provide signals from areas highly tuned to any visually responsive region. The contrast of coherent over incoherent motion yielded activation clusters of motion processing areas, specifically ones integrating coherent motion, such as area V6 (Cardin et al., 2012b), and MST/TO-2, a part of area of V5/MT+ (Huk et al., 2002) which shows bigger receptive fields, integrating motion. Heading direction of motion, V6 and MST/TO-2 show sensitivity to the change of field of flow (Cardin et al., 2012b). Area MT/TO-1 within the V5 complex is known to be activated about equally by any motion patterns (Smith et al., 2006). Blank periods help the BOLD signal return to baseline which is crucial in distinguishing activation tied to the specific condition shown. Incoherent motion provided a control condition for coherent motion, and contained random

dot motion. Incoherent motion blocks contrast coherent motion and identify areas which show even higher activity to coherent motion over incoherent motion. These areas include V6 as well as TO-2 (a subdivision of area V5/MT+), both areas possessing wide receptive fields which are vital in integrating coherent motion flow over larger visual field extents (Smith et al., 2006).

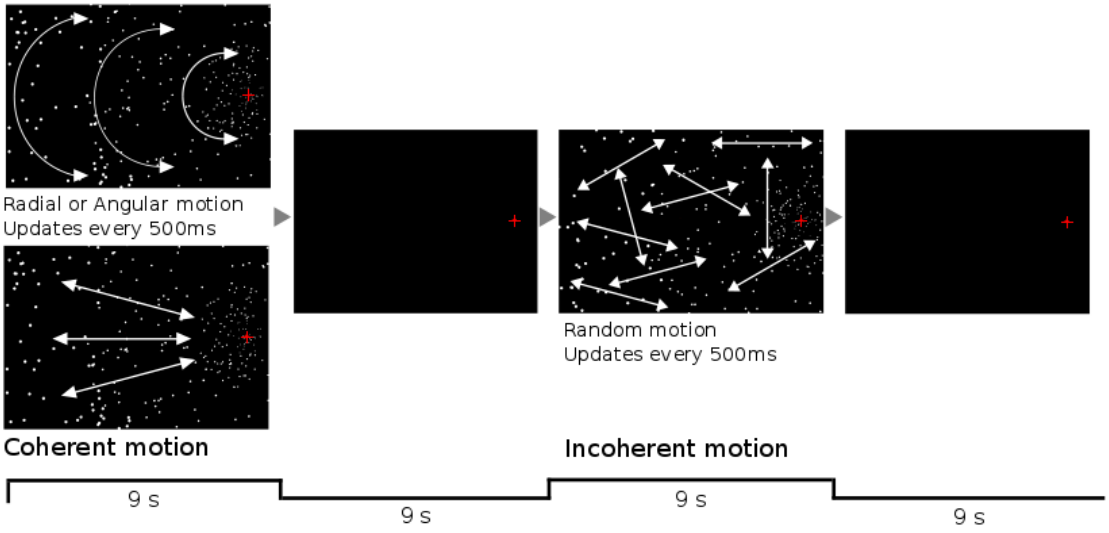

Figure 2.7 – A Schematic of an optic flow stimulus cycle. The coherent motion block consisted of four motion types (radial: expanding and contracting, and angular: clockwise and counter-clockwise) 100 % coherence (outlined above) these were presented in a random fashion, and updated every 500ms. Incoherent motion updated every 500ms and consisted of 100% randomly moving dots. The cycle was repeated 8 times.

2.11 Preprocessing of Visual Motion Data

Statistical analysis in each participants data was carried out using FEAT (part of FSL, FMRIB's toolbox, Oxford, UK; Smith et al., 2004, http://fsl.fmrib.ox.ac.uk/fsl/fslwiki/). The first 3 volumes (9s) of the scan were removed as the scanner reaches magnetic saturation during this time. Regressors for each condition-block in the GLM were convolved with a double gamma hemodynamic response function. Preprocessing of data included motion correction (MCFLIRT, FSL), spatial smoothing (Gaussian, FWHM, 4mm) and a temporal high-pass filter cut off (0.01Hz). First-level general linear model analysis (FILM) was then carried out, where regressors for each condition-block were convolved with a gamma haemodynamic response function. Each individual EPI sequence underwent time series

prewhitening (Smith et al., 2004), allowing us to carry through contrasts for higher level analysis to test for group effects . Individual subject GLM results were transformed into standard 2 mm resolution MNI 152 space, with the use of inplane structural scans (Smith et al., 2004).

2.12 ROI Analysis

For the motion stimulus data, the study compared differences in activation between the deaf and hearing participants, using the dependent measure of average BOLD percentage signal change across all voxels of the respective ROI. Activation was extracted for both coherent and incoherent motion blocks, relative to fixation baseline. It was extracted using Featquery within FSL (FMRIB toolbox). To carry this out, Featquery takes each participants high-resolution structural scan and co-registers it to the standard MNI152 2mm brain using FLIRT multi-registration

2.13 ROI Selection

2.13.1 Area V5/MT+

The V5/MT+ visual motion area was investigated with a region of interest (ROI) consisting of a sum of three previously established definitions of the area: a cytoarchitectonic definition of V5 by the Juelich Histological Atlas (Eickhoff et al., 2007) as well as functionally defined sub-divisions of area V5/MT+, TO-1 and TO-2, by Wang et al. (2015). Areas MT and MST refer to macaque divisions of area MT+, whereas human V5, contains functionally equivalent areas named TO-1 and TO-2 (Amano et al., 2009). The Eickhoff et al. (2007) ROI is based on a definition of V5/MT+ in 10 postmortem brains by Malikovic et al. (2007) resulting in a probability map of this area. They assigned each voxel to the most probable area at its location and, to increase precision, restricted the region to only include voxels assigned >10% probability (Eickhoff et al., 2007) see Figure 2.8.

The Wang et al. (2015) ROI definitions are functionally defined based on retinotopic mapping (based on previous selections by Amano et al., 2009). Amano and collegues

used motion localiser data to establish the location and extent of the subdivisions of area V5/MT+, namely TO-1 and TO-2. The masks used for our analysis were restricted to voxels assigned >15% probability. A stricter probability was used for this region as the unrestricted mask spans over a wide cortical area, and also wanted to ensure that the two sub-regions (TO-1/TO-2) overlapped substantially with the Juelich V5 definition (Eickhoff et al., 2007). The probability value established by (Wang et al., 2015) was calculated by dividing each node within the given ROI by the number of times those coordinates were located within the ROI by the number of participants included for the given ROI. This definition of TO-1 and TO-2 was based on 42-48 subjects. The value therefore provides the likelihood of a given node to be identified as part of the visual area. In the current study, a left and right V5 ROI was defined, consisting of the sum of voxels from Juelich Histological Atlas (Eickhoff et al., 2007) and Wang et al. (2015) definitions, within the standard MNI152 2mm brain (see Figure 2.8). The ROIs were combined with fslmaths, a function which is part of the FSL, FMRIB's toolbox (Smith et al., 2004). The standard definition was transformed into each individuals brain, and the activation extracted with Featquery in FSL. Together, these ROI masks provide a well encapsulating definition, being based on both cytoarchitecture and functional definitions. The mask also takes into account the asymmetry between hemispheres (see Figure 2.9).

2.13.2 Area V6

Area V6 is located within the parieto-occipital sulcus in each hemisphere. Previous research using wide-field retinotopic mapping revealed that V6 in each hemisphere has a full visual map of the contralateral hemifield and a large emphasis of the peripheral visual field (Pitzalis et al., 2006, 2010). The area is highly activated by coherent motion, especially motion which is egomotion compatible, providing motion in depth such as optic flow stimuli (Cardin and Smith, 2011). In our study, the V6 ROI was defined based on the activation cluster derived from contrasting coherent optic flow motion blocks over incoherent motion blocks (see Figure 2.10). V6 is a visual area which has been discovered during the last decade, and to our knowledge, there are no cytoarchitectonic of functional atlas definitions widely available to guide its definition. The area is also very focal, and occupies a small area of cortex, at the end of the parieto-occipital sulcus. The study therefore chose to create a spherical ROI mask in each hemisphere, based on group analysis including a

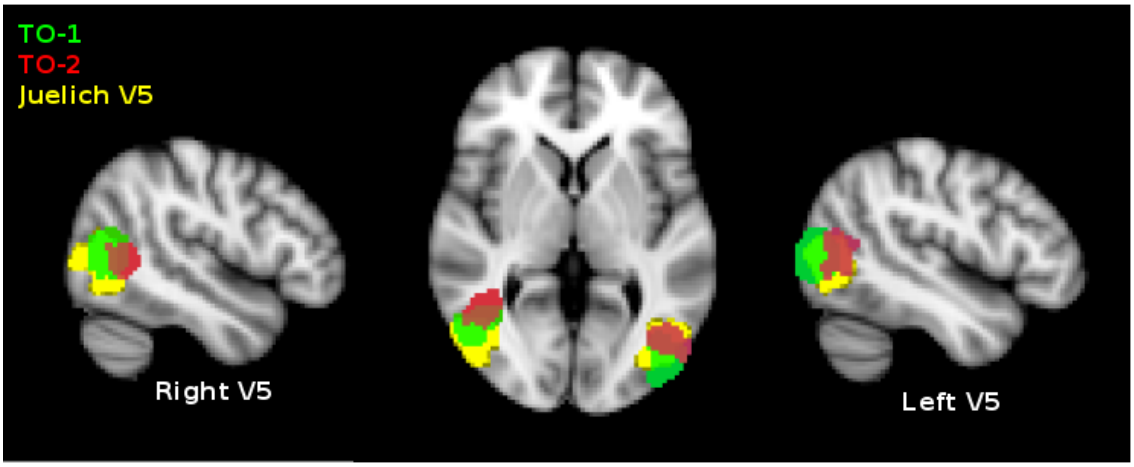

Figure 2.8 – Combined V5 ROI as defined within the standard MNI 152 brain (2 mm voxel resolution. The masks above show the Juelich atlas and (Wang et al., 2015) definitions of the total area of V5 (in yellow), as well as TO-1 (green) and TO-2 (red) which are two known functional subdivisions of the V5/MT+ complex.

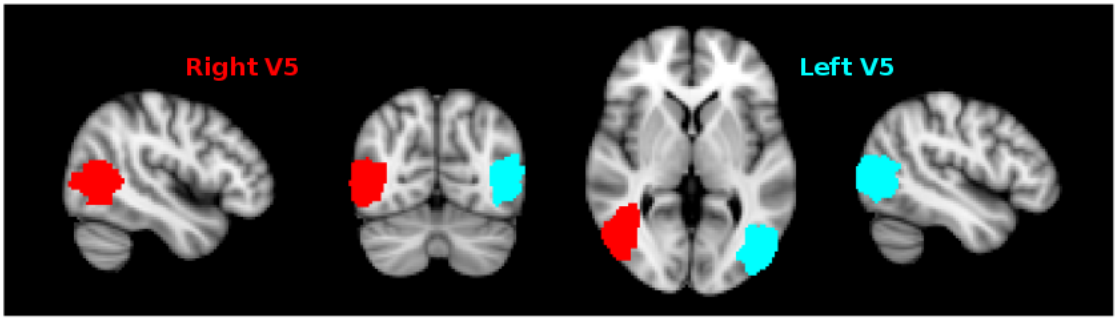

Figure 2.9 – Left and right V5 ROI masks used in analysis, which are constituted of the Juelich cytoarchitectonic atlas (Eickhoff et al., 2007) as well as definitions of TO-1 and TO-2 by (Wang et al., 2015) represented on the MNI 152 brain.

total of 40 both deaf and hearing participants.

Each individuals fMRI data were processed using FEAT (FMRI Expert Analysis Tool) Version 6.00, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Preprocessing of the data included motion correcttion with MCFLIRT, spatial smoothing using a Gaussian kernel of FWHM 4mm and a high-pass temporal filter (cutoff, 0.01 Hz). The first-level general linear model (FILM) analysis tool was used on each individuals functional data with time series pre-whitening (Woolrich et al., 2001). These data were transformed into standard MNI152 2mm brain space (Jenkinson et al., 2001). Higher-level analysis of all 40 participants was done with FLAME Bayesian mixed-effects analysis (Beckmann et al., 2003). The inplane structural scan was used in a co-registration process (FLIRT; Jenkinson et al., 2001) to transform the functional images to the high resolution T1 structural scan.

Group analysis was carried with 13 deaf and 27 hearing participants with the FMRI Expert Analysis Tool, which is part of the FSL, FMRIB's toolbox

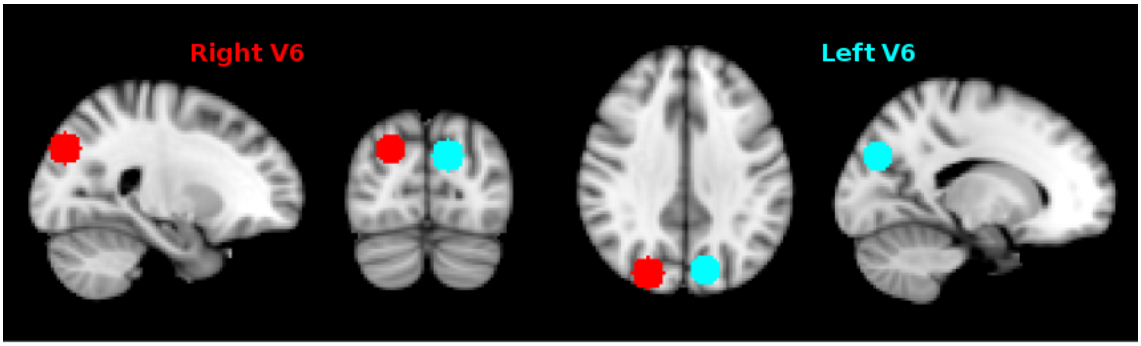

Figure 2.10 – Left and right V6 sphere ROI used for analysis. The sphere ROIs are both 10mm in diameter, grown around the center of gravity of the group activation cluster derived from the coherent > incoherent motion contrast, p<.05.

The group activation clusters were extracted from the contrasting of coherent>incoherent motion blocks from the optic flow functional MRI scan. An ROI sphere (10 voxel diameter, $2mm^3$ voxels, 2cm sphere diameter) was built around the COG voxel (Figure 2.10). This spherical ROI defined in MNI standard space was then transformed back to each individuals anatomical space using FLIRT (FSL toolbox). Our V6 coordinates, as (Stenbacka and Vanni, 2007), where reported bilaterally also show that V6 is located slightly lower in the

Table 2.2 – MNI coordinates (mm) of area V6 found in previous studies. Stenbacka and Vanni (2007) provide coordinates of V6 within both hemispheres, whilst the remaining research provides it unilaterally

Coordinates - x,y,z		
Left V6	Right V6	Authors
-11,-77,46	N/A	(Pitzalis et al., 2006)
N/A	9,-82,36	(Pitzalis et al., 2010)
-12,-77,37	18,-77,34	(Stenbacka and Vanni, 2007)
-12,-78,32	24,-80,34	Current study

right hemisphere. Our coordinates vary somewhat from those defined by previous studies, particularly within V6 in the right hemisphere (Table 2.2). As the region is focal, it is crucial to base the definition on the group analysis. Defining the ROIs based on previous literature could have caused a failure to detect crucial activation within V6.

2.13.3 Auditory Cortex

When investigating cross-modal plasticity in the auditory cortex of deaf individuals, fMRI studies query a variety of predefined cortical regions. The Harvard-Oxford Cortical Structural Atlas (Harvard Center for Morphometric Analysis) includes definitions of primary auditory cortex, Heschl's gyrus, as well as secondary auditory and somatosensory area Planum Temporale (PT). The Juelich histological atlas (Eickhoff et al., 2007) contains definitions of primary auditory cortex (Te1) where it is divided into three distinctive areas, namely: Te1.0, Te1.1 and Te1.2. These areas are based on the microstructural analysis of HG in 10 post-mortem brains (Morosan et al., 2001).

In the current study, three separate regions of interest within auditory cortex were chosen to measure the response profile to visual optic flow motion stimuli. The three regions were chosen in order to separate the broader auditory area along the Sylvian fissure, superior or inferior to Heschl's gyrus, to include regions representing primary, secondary and associated auditory regions. As explained previously (section 1.9), effects of plasticity observed due to auditory deprivation can be seen in various regions within the auditory cortex (Fine et al., 2005). It is possible that regions which are multisensory in their processing of sensory signals show higher levels of plasticity in deaf individuals when processing motion stimuli than regions which process sensory inputs in a unimodal fashion, as shown in previous literature concerning plasticity within auditory cortex in the deaf

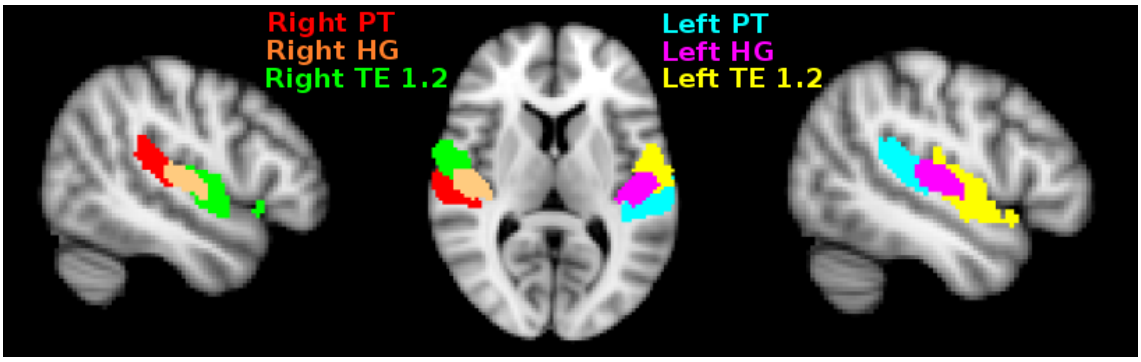

Figure 2.11 – Left and right auditory cortex masks, TE 1.2 from the Juelich citoarchitectonic atlas (Eickhoff et al., 2007), PT (Planum Temporale) and HG (Heschl's Gyrus) from the Harvard-Oxford Cortical Structural Atlas represented on the MNI 152 brain.

brain (Lomber et al., 2010).

Firstly, the study included Heschl's gyrus (HG) as it would correspond to the core of primary auditory cortex, and overlap substantially with the Te 1.0 region, as defined in the Juelich atlas (Eickhoff et al., 2007). A quantitative analysis of myelination across Heschl's gyrus (Dick et al., 2012) showed that the highest myelination was found within the medial section (2/3) of the HG region, area Te 1.0. In order to ensure HG focal nature, a restricted version of the HG ROI was used (<20% probability, see Figure 2.11).

Secondly, the Harvard Oxford cortical definition of Planum Temporale was chosen. The area is located slightly posterior to the auditory cortex (HG) within the Sylvian fissure. PT is very asymmetric, and can vary tenfold and is usually larger in the left hemisphere (Rademacher et al., 2001)(see Table 2.3). This area has previously been used to identify cross-modal plasticity in deaf individuals (Fine et al., 2005, Shiell et al., 2010), and is involved in auditory and language processing. Additional neuroimaging studies show its involvement in auditory spatial localisation (Warren et al., 2002). The study restricted the region of PT to above 10%, as the unrestricted region covers a very wide extent of temporal cortex, spanning from the superior temporal gyrus all the way along the Sylvian fissure to the supramarginal gyrus. The region was restricted in order to include more secondary auditory areas, STG (superior temporal gyrus) and STS (superior temporal sulcus). The ROI also includes Wernickes area (posterior STG), essential for language comprehension. As the modality of language differs significantly between deaf and hearing individuals, this region can show high levels of plasticity.

Table 2.3 – Sizes of the auditory ROIs used in analysis, as defined in standard space (MNI 2mm brain, 1 vox = 2mm). used to extract mean percentage BOLD signal changes to visual motion.

	Left Hemisphere		Right Hemisphere	
ROI	number of voxels	mm^3	number of voxels	mm^3
V5	1997	15976	1937	15496
V6	515	4120	515	4120
TE 1.2	1263	10104	934	7472
Planum Temporale	1464	11712	1242	9936
Heschl's Gyrus	477	3816	430	3440

Finally, area Te1.2 was also included. It is localised anterior of the core of HG, which shows broad lateral connections in layer III, which contains clusters of medium sized IIIc pyramidal cells (Morosan et al., 2001). These in turn can also be seen in non-primary auditory areas, which could indicate connections with auditory areas implemented in spatial processing of auditory motion. Area Te1.2 was chosen as it is part of HG, however its structure of IIIc pyramidal cells resemble a similar profile seen in non-primary auditory areas (Morosan et al., 2001). This ROI was not restricted, as it is focal in its existing definition. As these regions are placed in near proximity, any possible overlaps between the ROIs were removed with fslmaths (Smith et al., 2004, part of the FSL, FMRIB's toolbox;). This was done to ensure that activation measured within each region did not 'leak' into activation measurements of the other two auditory regions.

2.14 Psychophysical Experiments

Psychophysical testing measures the thresholds and abilities of our perceptual systems. Two psychophysical experiments were used to investigate far-peripheral visual motion sensitivity within our deaf and hearing participants. These included a global motion discrimination task and a local motion detection task.

2.15 Global Motion Discrimination Stimulus

The global motion discrimination task consisted of stimuli designed to stimulate the far-peripheral visual field and test motion direction discrimination of coherent motion within incoherent motion noise. The task was designed based on stimuli known to highly activate

V6 (Pitzalis et al., 2006; Cardin et al., 2012a) and area V5/MT+ (Smith et al., 2006), which were speculated to be correlates of global motion discrimination performance, and possible substrates of higher sensitivity in deaf individuals. The task consisted of three conditions testing the central visual field, left hemifield and right hemifield. Within each of these, the participants task was to judge the direction of motion within either radial or angular motion trajectories, and these two motion types were presented in separate runs. The size of the moving dots was scaled according to eccentricity, to account for cortical magnification (Cowey and Rolls, 1974) as well as create the illusion of motion in depth (optic flow). Within the central condition, the motion stimulus comprised of dots, sized 12 arc min (0.2 °), with a density of 0.5 dots/deg ^{2}. Each dot moved at a speed of 5 °/s. These stimuli were presented within an aperture with a 5 ° radius around central fixation (a red '+' sign, 0.5 ° in size). The far-peripheral condition contained dots sized 55.2 arc min (0.92 °), with a density of 0.3 dots/deg ^{2}. Each dot moved at a speed of 50 °/s. The stimuli were presented in an aperture extending beyond the edge of the screen, with a fixation target situated either at -40 ° or +40 ° horizontally shifted off centre, such that each hemifield was tested separately. In order to target the far-peripheral visual field only, the central part of the aperture was masked, in order to display motion only beyond 40 ° from fixation, extending to the edge of the screen, at 89 ° (see Figure 2.12). The dots were white (198.8 cd/m ^{2}) displayed on a mean luminance background (99.9 cd/m ^{2}), and stimulus presentation lasted for 500ms, the next commencing after a response was given. Radial and angular motion conditions were tested in separate 2AFC runs, where participants judged the perceived direction of dot motion to be either clockwise/counter-clockwise for the angular condition and inwards/outwards during the radial condition. Responses were recorded through a keyboard, and participants used their preferred hand to respond.

2.16 Local Motion Detection Stimulus

The local motion task was designed to test the sensitivity of local motion detection at different eccentricities, including the far-periphery, in contrast to the global motion discrimination task. Previous studies with localised motion tasks have reported visual processing advantages in deaf human subjects (Hauthal et al., 2013; Shiell et al., 2014; Scott et al., 2014) and deaf cats (Lomber et al., 2010). The stimulus used consisted of two

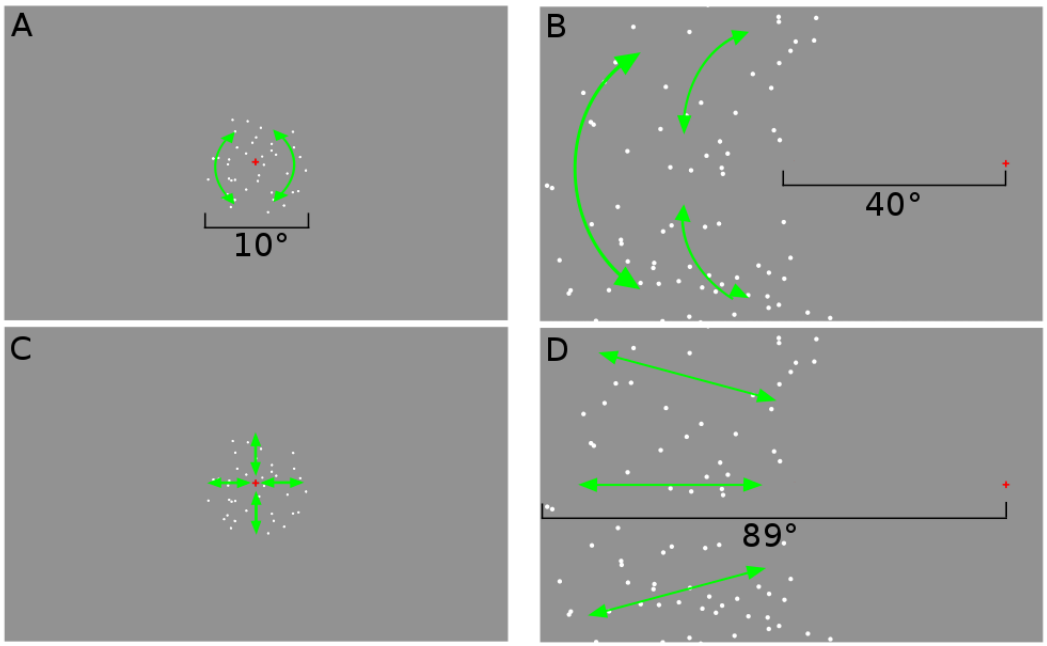

Figure 2.12 – A schematic representation of two eccentricity conditions (central: A, C; left peripheral B,D). The green arrows represent the two possible directions of motion, it being either angular, clockwise/counter-clockwise (A, B) or radial, inwards/outwards (C, D). The right peripheral hemifield condition was a mirror image of the left hemifield condition. The green arrows indicate the two possible angular motion directions (clockwise and counter-clockwise directions). The coherently moving dots would be amongst incoherently moving ones, where the percentage of coherently moving dots necessary for 75% correct responses was extracted as the motion discrimination threshold.

apertures, 9 ° in diameter, on either side of the fixation cross. There were four conditions, where the dot apertures were positioned centred at either 5 °, 10 °, 20 ° or 40 ° away from fixation (a red '+' sign, 1 ° in size), on the horizontal meridian. Each aperture contained 30 dots, 0.5 ° in size, with a dot density of 0.47 /deg ^{2} and the dots had a Gaussian envelope (0.1 deg sigma) (see Figure 5.6). The envelope was applied to the dots as well as the aperture to minimise the use of the edge from providing cues to influence participants judgements. They were white (198.8 cd/m ^{2}), presented on a mean luminance background, (99.9 cd/m ^{2}) giving a 50% contrast. The motion trials were presented for 500ms, the dots having a limited lifetime of <500ms to minimise tracking of single dots, to ensure that participants detected motion by net motion judgements.

To ensure stable fixation, participants were given clear instructions and their performance was monitored in person during training, as eye movements were not monitored. A previous study observed that deaf participants appear to have a higher level of fixation stability than hearing individuals (Codina et al., 2011b). In each trial, one of the two apertures would contain dots moving randomly either left or rightwards with 100% dot coherence. Participants were instructed to indicate which of the apertures contained motion (left or right aperture), but not the direction of dot motion. The next trial would begin after the response was given.

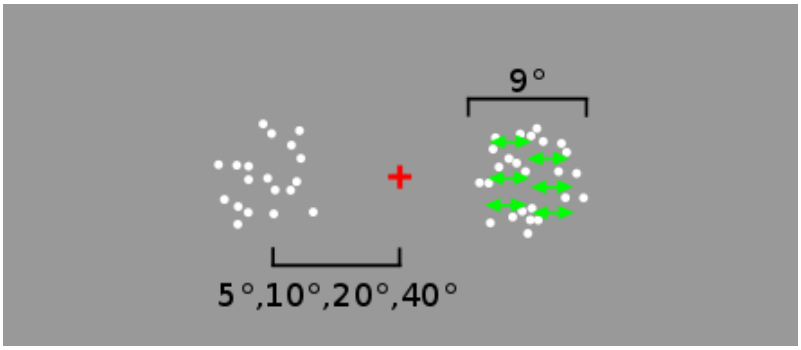

Figure 2.13 – A close-up schematic of the local motion detection task. The bilateral dot clusters were positioned 5, 10, 20 or 40 degrees away from fixation on each side, contained 30 dots with a Gaussian envelope. One of the two dot clusters would contain either leftward or rightward 100% motion.

2.17 Procedure

Both psychophysical tasks used the method of two alternative forced choice (2AFC), and were designed in Psykinematix (Beaudot, 2009). Subjects were seated in front of a Samsung 51 plasma display (dimensions of 1188 mm x 707 mm, resolution: 1680x1050 pixels) in a dark room seated at a viewing distance of 600mm. Before commencing the experimental trials, the subjects were familiarised with the design with practice trials. Each participant went through practice trials for one 5 ° and one 20 ° condition in the local motion task and one peripheral and one central condition in the global motion task (hemifield chosen at random). Each run in each condition included 100 trials in total, where the first 10 allowing for training and not included in the fit of a Bayesian adaptive Weibull staircase (Kontsevich and Tyler, 1999). In the global motion task samples were taken between 0-100% coherence in steps of 1.875 (40 samples), and in the local motion task, between speeds of 1 °/s - 0.001 °/s in steps of 0.025 (40 samples). The experimenter was present during this practice period to make sure the participant understood the procedure, as well as provided an opportunity for participants to ask questions. When testing deaf subjects familiar with BSL, a BSL interpreter assisted in explaining the task if further clarification was needed. The order in which participants carried out the different conditions was randomised to avoid practice effects as a possible confound. Every participant carried out each condition at least twice, if the thresholds were in close agreement. If the thresholds were not, participants completed additional runs to ensure closer agreement of thresholds. Before each run, participants were prompted with written instructions on screen, where they were reminded to fixate on the cross at all times. Responses were recorded through a keyboard. Participants chose to respond with their preferred hand. Testing each participant took 40-60 minutes per task, depending on breaks taken between runs and explanation time needed.

2.18 Preprocessing of Psychophysical Data

In the global motion task, the threshold obtained indicated the percentage of coherently moving dots relative to randomly moving dots within the aperture. The percentage of coherently moving dots was varied per trial to establish a coherence threshold, meaning

the percentage of coherent-motion signal yielding responses at 75% correct. The threshold from each run was then averaged across runs within each condition to provide a mean for all motion sensitivity within a visual location. These included means for the radial and angular motion runs within the central, left and right peripheral locations. In the local motion detection task, the threshold was based on the minimum speed necessary for 75% correct detection. Thresholds extracted were averaged across runs, to provide one mean threshold for each eccentricity condition. For both tasks, a Bayesian adaptive Weibull staircase paradigm was used to extract thresholds (Kontsevich and Tyler, 1999). The mean median reaction times were recorded for the correct response trials in each condition for both tasks. Responses given before 200ms were discarded, attributed to premature responses or a lapse in attention.

2.19 Adaptive Staircase - 2AFC Weibull Function

To establish the motion sensitivity threshold in both psychophysical experiments an adaptive Bayesian staircasing procedure was used, developed by Kontsevich and Tyler (1999) and implemented in Psykinematix. This is a way in which a variable level (speed or type of motion) selected at each trial is determined by the observers responses on previous trials, extracted from the posterior probability distribution of values sampled across the psychometric function (Figure 2.14).

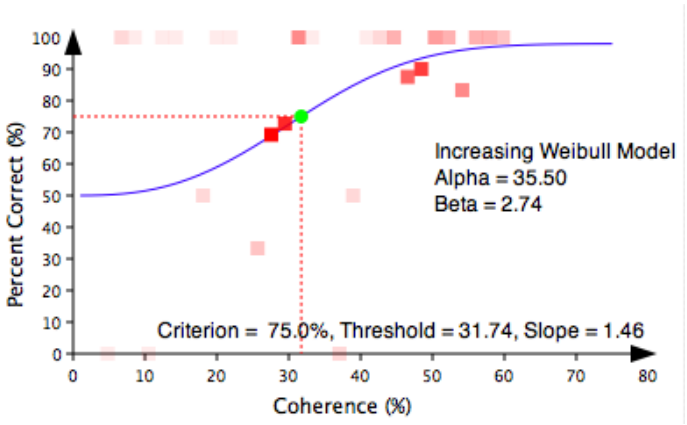

Figure 2.14 – Example psychometric function representing an increasing weibull model used to extract a perceptual threshold, from Psykinematix (Beaudot, 2009).

The sensitivity of the function is controlled by two parameters: alpha, which determines

the overall position of the psychometric function along the abscissa of the psychometric function, and beta, which determines the slope of the curve. As the Bayesian adaptive staircase method converges quickly to produce asymptotic estimates of both the alpha and beta parameter, only 100 trials or fewer were needed to reach a threshold. The method used requires fewer sessions compared to a standard staircasing procedure where more sessions are usually needed, producing more variable estimates of the threshold. The method allows us to 'home in' on the individuals detection or discrimination threshold and restricts the number of trials presented, minimising the presentation of trials that are either to easy or too difficult, concentrating the trials around threshold values to improve estimates. This is vital as the present study had limited access to congenitally deaf subjects. A large number of our deaf participants travelled from different cities to take part in this study. All testing would often take part during one day, as time was limited it was crucial to maximise data collection efficiency and minimise participant fatigue. Each trial lasted approximately 3-4 minutes and consisted of 100 trials, and the threshold convergence only began after the first 10 trials.

Chapter 3

Visual Field Representations in Visual Areas of Deaf and Hearing Adults

3.1 Overview

This chapter describes the first empirical experiment which investigated intramodal plasticity within the visual cortex of deaf adults compared to hearing controls. The chapter begins with a brief background describing previous evidence of cortical plasticity within deaf individuals. The experimental hypotheses are then outlined, followed by a brief description of of wide-field retinotopic mapping methods used in fMRI. The results are described with a focus on the distribution of visual field representations within primary visual cortex, known as V1, as well as visual areas V2 and V3.

3.2 Background

The loss of one sensory modality can lead to changes in behavioural performance which relies on the remaining sensory modalities. A number of studies show behavioural advantages in congenitally deaf individuals, especially in processing of visual motion in the peripheral visual field (Neville and Lawson, 1987; Bavelier et al., 2000; Proksch and Bave-

lier, 2002; Hauthal et al., 2013; Heimler and Pavani, 2014; Shiell et al., 2014, Loke and Song, 1991).

In line with behavioural changes, a multitude of evidence shows that auditory deprivation can lead to large-scale cortical reorganisation (Heimler and Pavani, 2014; Sadato et al., 2005, Bottari et al., 2012a). This plasticity in the deaf is seen in a number of cortical regions, such as motion area V5/MT+ (Scott et al., 2014, Bavelier et al., 2001) and auditory cortex during visual presentations of motion (Finney, 2001; Armstrong et al., 2002; Fine et al., 2005; Lomber et al., 2010; Meredith et al., 2011; Vachon et al., 2013; Bottari et al., 2014). In addition to differences in V5/MT+ and auditory cortex, when presenting deaf and hearing participants with peripheral visual stimuli, the superior temporal sulcus (STS) also shows increased activation in deaf participants compared to hearing controls (Scott et al., 2014). Cross-modal processing involving visuo-somatosensory stimuli also show increased activation of auditory cortex in deaf individuals (Karns et al., 2012).

The aforementioned studies outlining various behavioural and neural findings do not generally investigate the peripheral visual field beyond 30 ° of eccentricity. From an ecological perspective, auditory cues are useful in directing hearing individuals to events in the far-periphery or even outside of the visual field. As deaf individuals lack this input, one could expect that deaf individuals benefit the most from higher visual sensitivity beyond 30 °. The peripheral representations are more likely to accommodate these sensory changes, as Burnat (2015) explains that visual peripheral processing shows higher levels of plasticity throughout life, in contrast to central vision, which is solidified during earlier stages of development. Buckley et al. (2010) show support for this, as they found strongly significant behavioural differences between deaf and hearing individuals in the far periphery. Visual field sensitivity was measured with a Goldmann kinetic perimetry test extending out into 90 ° into the periphery. Both near peripheral (around 30 °) and far-peripheral (around 60 °) visual field processing advantages were found in deaf participants, when compared to hearing controls.

Where can substrates responsible for this behavioural advantage be found? Before discussing possible substrates of this heightened sensitivity in the brain, Codina et al. (2011b) investigated the early visual pathway of deaf individuals with use of optic coherence tomography (OCT). The researchers showed structural differences in the early visual pathway, where deaf individuals demonstrated a larger neuroretinal rim area, the region in which

ganglion cell axons exit the eye. In addition, portions of the retinal nerve fibre layer (RNFL) containing projections from the peripheral retina were significantly thicker in deaf participants Codina et al. (2011b). The RNFL thickness within both hearing and deaf participants correlated directly with behavioural measures of peripheral visual field sensitivity in both the far-peripheral (60 °) and near-peripheral (30 °) conditions. This provides evidence of early-visual structural differences of the retina relating to visual processing advantages specific to the near and far-peripheral visual field.

As mentioned, Codina et al. (2011a) have shown early visual stream differences in the retina of deaf individuals, as well a thicker retinal nerve fibre layer in the peripapillary regions which contain neurones processing the temporal retina (peripheral projections). Changes seen this early in the visual stream indicate a possible difference downstream where these signals are received, in primary visual cortex (V1).

It is still uncertain whether deaf adults show an overall size difference in V1, V2 and V3, relative to hearing controls. An early study showed no differences in overall V1, V2 and V3 size between deaf and hearing participants (Fine et al., 2005). Another study investigating the structural cortical differences between deaf and hearing individuals by Allen et al. (2013) report that deaf participants have a larger volume in the calcarine cortex (the site of V1) compared to hearing individuals. The volumetric measurements mentioned consist of both the cortical thickness measurement and surface area. Song et al. (2015) suggest that the two dimensions measuring cortical volume, namely thickness and surface area, contribute to processing advantages in different ways. A larger surface area, and thinner cortex correlated with visual perceptual advantages in their study. Another fMRI study reported that deaf adults have a thinner cortex within the peripheral representation of V1 (Smittenaar et al., 2016). In the current study, measures of surface area and thickness were extracted to investigate if and how these two cortical dimensions reflect plasticity as a result of hearing loss. The above mentioned fMRI studies by Fine et al. (2005) and Smittenaar et al. (2016) were based on visual field mapping extending to 15 ° and 37.5 ° respectively, and did not incorporate the far peripheral visual field representation where the behavioural enhancement seems most prominent. It is essential to expand on current research by including measurements of far-peripheral cortical representations (up to 72 ° in this experiment) in order to explore neural substrates of the behavioural advantage seen in the far eccentricities. As a result of sensory loss, these regions of visual

areas are likely to exhibit signs of plasticity, possibly in shape of larger overall visual field representations, or a larger amount of cortical surface area devoted to the periphery, relative to the central visual field. It is important to note that the size of V1 can vary up to threefold between individuals (Andrews et al., 1997; Dougherty et al., 2003). Previous studies have related V1 size to perceptual differences (Schwarzkopf and Rees, 2013), as well as related cortical magnification functions of V1 with acuity thresholds on an individual level (Duncan and Boynton, 2003). Therefore, if structural differences between deaf and hearing adults are found in early visual cortex, it could directly relate to their behavioural visual enhancements reported in previous studies.

This study also included measures of visual areas V2 and V3 as few studies investigate if the structure and function of these areas can also exhibit plasticity as a result of deafness. Areas V2 and V3 are well defined early visual areas with clear visual field representations and are easily measured with retinotopic mapping procedures. V1 and V2 are still highly correlated and can be traced to individual differences in optic tract surface, as presented by Andrews et al. (1997). Primate studies show that V3 is not related to the earlier visual areas in the same manner, hence it is likely that its surface area depends on other inputs, possibly from central locations or neural connections passing through V2 but bypassing V1 (Sincich and Horton, 2005). Furthermore, functional specialisation of visual areas V2 and V3 has been investigated in neurotypical individuals, for example, Marcar et al. (2000) showed that V2 cells in the macaque are specifically tuned to boundary information as defined by motion, specific to the orientation of that boundary. Likewise, research in humans suggests that V2 could be involved in the detection of border ownership (Zhou et al., 2000). A recent study also showed the specialised involvement of V2 in the processing of naturalistic image structures (Freeman et al., 2013). As V2 and V3 receive strong inputs from V1, and if plasticity is seen in V1, it is likely that these regions will also be influenced as a result. On one side, it is possible that V2 and V3 will mirror any effects seen in V1, or, as the regions are more extrastriate visual areas, they could display higher levels of plasticity.

Other possible factor influencing plasticity in the deaf population could originate from changes in cross-modal connections between auditory and visual cortices. Peripheral visual projections also show specific interconnections with auditory cortex. Falchier et al. (2002) show direct connections between the primary visual and auditory cortex within

hearing primates. Therefore, visual information can reach the auditory cortex, however these signals could be strengthened in deaf individuals due to a higher reliance on visual cortex. The visual cortex is organised in a hierarchical fashion, and the effects mentioned in higher visual areas are likely to be underpinned by changes occurring earlier in the visual stream.

3.3 Summary and Hypotheses

The goal of the current study was to investigate the possibility of intramodal plasticity within primary visual cortex as a result of lifelong auditory deprivation, which might underpin visual advantages found within the far-periphery of deaf individuals (Buckley et al., 2010; Codina et al., 2011a). Based on evidence that visual field sampling is altered in the retina in congenitally, profoundly deaf individuals, it was hypothesised that there will be differences in the distribution of visual field representations between deaf and hearing groups within primary visual cortex, V1, as well as V2 and V3. Using functional MRI to measure visual field maps in these visual areas, one would expect to see thinner cortex within peripheral representations in deaf, compared to hearing individuals. In line with this, one would also expect to see a relatively greater representation of the visual periphery, relative to the central representation, in deaf, compared to hearing participants.

3.4 Methods

3.4.1 Participants

The study included 32 subjects: 16 congenitally and profoundly deaf individuals (mean age=34.13, range=20- 48 years, 5 females, see Chapter 2, Table 2.1 for more details) and 16 hearing individuals (mean age=29.61, range=20-48 years, 5 females). There was no significant difference in age between the groups ($t(30)=1.291$, $p=.207$). All participants had normal or corrected-to-normal vision and gave informed consent. Each deaf participant also filled out a brief questionnaire regarding the known aetiology of deafness (Chapter 2, Table 2.1). All deaf participants reported severe to profound hearing loss in both ears (>70db). The study was approved by The York Neuroimaging Centre Research Governance Committee (Department of Psychology, University of York).

3.4.2 Data Acquisition

3.4.2.1 Imaging Parameters

Participants underwent between one and three scanning sessions, during which functional and structural MRI data were acquired using a 16 Channel Posterior Brain Array coil (Nova Medical) in a GE 3 Tesla Signa Excite HD scanner at the York Neuroimaging Centre. The structural data were acquired with high resolution T1-weighed structural isotropic scans, the functional data were acquired with a BOLD T2* EPI sequence. Two additional structural scans were acquired: an inplane proton density scan for all participants and T2* gradient echo scan for a subset of six participants, to aid structural data analysis described in Chapter 2, Section 2.3.

3.4.2.2 Retinotopic Mapping

The following experiment was designed to map the far peripheral visual field representation, where visual sensitivity was greatest in deaf participants (Buckley et al., 2010; Codina et al., 2011b). To examine this, visual maps that included the far peripheral representation were extracted through means of retinotopic mapping in fMRI (DeYoe et al., 1996,

Sereno et al., 1995, Engel et al. 1997). Neural substrates involved in far-peripheral visual processing are challenging to identify as neuroimaging, particularly functional magnetic resonance imaging (fMRI) imposes methodological constraints. For example, the field of view possible to stimulate is limited by the size of the bore in which the participant lies (for more detail see Chapter 2, Section 2.4). This study introduces a novel way of reliably mapping the far-peripheral visual field of both deaf and hearing individuals, extending out to 72 ° in each hemifield. Wide field phase encoded retinotopic mapping stimuli encompassing 144 ° of the visual field (adapted from DeYoe et al., 1996, Sereno et al., 1995, Engel et al. 1997) measured the cortical representation of polar angle (0 °-180 °, starting at the upper vertical meridian in the right hemifield, and lower vertical meridian in the left hemifield) as well as the eccentricity (distance from centre of gaze) in the visual field of each participant. The stimuli were designed in Psykinematix (Beaudot, 2009). Chapter 2, Section 2.5 describes the design in detail.

3.4.3 Data Analysis

Structural images were processed and used as underlays to determine the anatomical boundaries of visual areas V1, V2 and V3, based on retinotopic mapping, within both hemispheres of each participant. This step measured the volume (mm^3), surface area (mm^2), and thickness (mm) of each visual area, as well as the eccentricity defined sub-ROIs within these. The structural and functional data were processed according to methods described in Chapter 2, Section 2.6.

3.5 Results

In order to investigate possible hemispheric differences in volume in early visual areas, a factorial mixed ANOVA was conducted with within subject factors of hemisphere (left, right) and visual area (V1, V2, V3) with a between subject factor of group (deaf, hearing). The test showed no main effect of hemisphere ($F(1,29)=.569$, $p=.457$, $\eta 2=.019$) or interaction between hemisphere and group ($F(1,29)=2.798$, $p=.105$, $\eta 2=.088$), thus the data from the left and right hemisphere were combined in each participant. The same test was conducted with the surface area measure. No main effect of hemisphere was

shown (F(1,29)=.3.901, p=.058, η2=.119), or interaction between hemisphere and group (F(1,29)=3.266, p=.081, η2=.101). Surface area measurements were combined across hemispheres.

3.5.1 Total Volume of V1, V2 and V3

Firstly, the overall volume differences between visual areas were investigated by extracting the absolute cortical volume of each visual area in all participants. Our aim was to identify any differences between deaf and hearing participants within visual areas V1, V2 and V3. One hearing participant was not included in V2 and V3 measures, as it was not possible to identify these regions in the left hemisphere. The polar angle data which guides the detection of visual field representation boundaries did not yield visible reversals of the stimulus when overlaid on cortical flat maps (for more detail see Section 2.7). In order to quantify the entire cortical visual field map, the volume measure in each participant was summed across hemispheres. To investigate these measures, a factorial mixed ANOVA with a between subjects effect of group was used. Mauchly's test showed that sphericity of the data was not met ($X^2(2) = 19.61$, p<.001; ε= .496) and the Greenhouse- Geisser correction was therefore applied. The ANOVA showed a strong significant difference in cortical volume between visual areas, F(1.330, 38.576)=110.95, p<.001, η2=.793. There was no significant interaction between visual area and group, F(1.330, 38.576)=1.364, p=.260, η2 =.045. Overall, there was no significant difference in the total cortical volume of V1, V2 and V3 between deaf and hearing participants, as shown by a test of between-subjects effects, F(1,29)=1.975, p=.171, η2=.064. Firstly, the results confirm, in line with the vast literature on visual field maps, that V1, V2 and V3 significantly differ from each other in cortical volume and cortical surface area. Secondly, there was no sign of volumetric differences between deaf and hearing participants, as indicated by the absence of interaction between the variables of volume and group.

3.5.2 Total Surface Area of V1, V2 and V3

To disentangle the volumetric measure which consists of both surface area and cortical thickness, measures were extracted of the absolute surface area of each visual area in all participants, excluding one hearing participant from V2 and V3 analysis (as mentioned

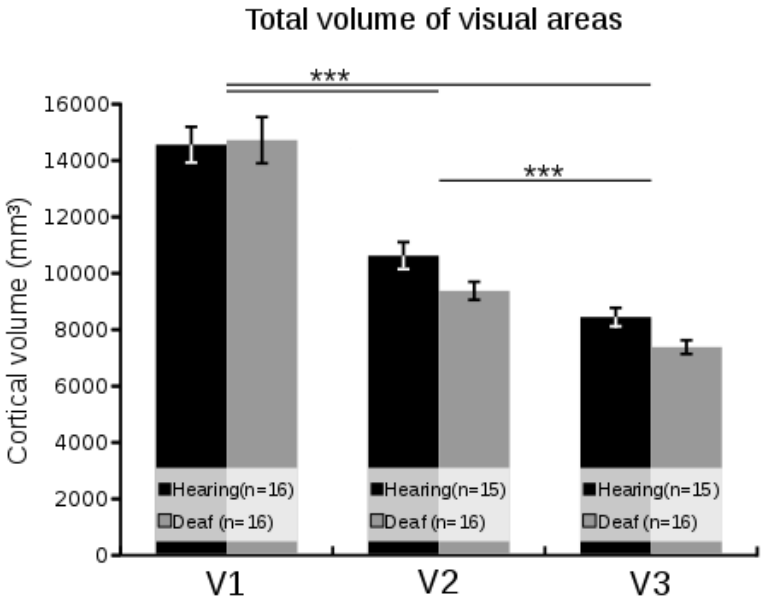

Figure 3.1 – A graph representing mean cortical volume values of each visual area V1, V2 and V3 in the deaf and hearing groups. ***=p<.001. Error bars represent 1+/-SEM.

in the previous section). The surface area measure was summed across hemispheres in each subject. Sphericity was not assumed ($X^2(2) = 8.12$, p= .017; ε= .748), hence the Greenhouse-Geisser correction was used. A factorial mixed ANOVA, with a between subjects effect of group, showed a strong significant difference between the visual areas in all subjects, F(1.598,46.340) =155.68, p<.001, η2=1. There was no significant interaction between visual area and group, F(1.598,46.340)=2.27, p=.124, η2=.393. No overall significant difference was seen in the total surface area of V1, V2 and V3, between deaf and hearing participants, F(1,29)=1.67, p=.210, η2=.239. As seen in the volume measure, pairwise comparisons of the surface areas in all participants showed V1 to be significantly larger in volume than V2 and V3, p<.001. Area V2 was also significantly larger than V3, p<.001 (see Figure 3.2). As with the cortical volume measure, V1, V2 and V3 significantly differ from each other in cortical surface area. As seen in the volume measure, there was no sign of surface area differences between deaf and hearing participants, as no interaction was present between the two variables (surface area, group).

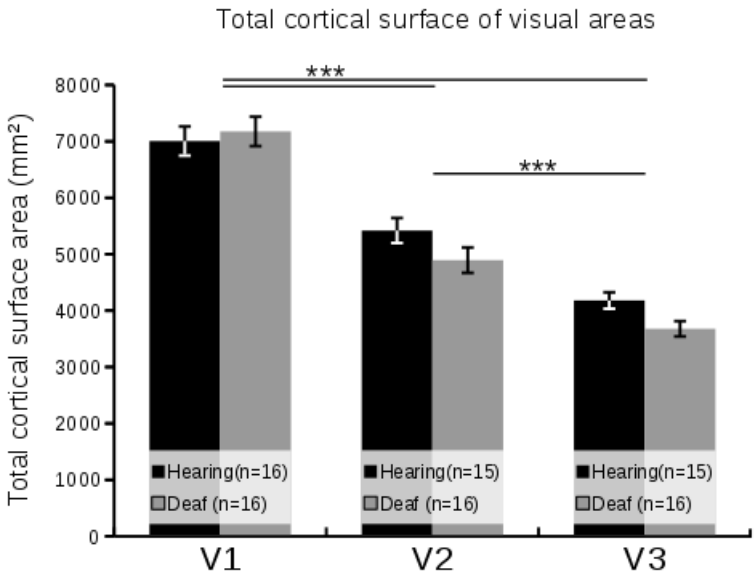

Figure 3.2 – A graph representing mean cortical surface area values of each visual area V1, V2 and V3 in the deaf and hearing groups. ***=p<.001. Error bars represent 1+/- SEM.

3.5.3 Mean Grey Matter Thickness in V1, V2 and V3

All participants were included in the analysis of grey matter thickness, as the comparisons were made with mean thickness values. The right hemisphere mean was used for the one hearing participant with no definable left hemisphere V2 and V3 visual maps. To test the differences in mean grey matter thickness, a factorial mixed ANOVA was used, with a between subjects effect of group. Sphericity was assumed, ($X^2(2) = 2.407$, p=.300; ε= .920) and the ANOVA showed a significant main effect of grey matter thickness across the visual areas, F(2,58)=7.210, p=.002, η2=.923. There was no significant interaction between visual area and group (F(2,58)=.482, p=.620, η2=.125). There were no significant between subjects effects, indicating no differences between the deaf and hearing groups in the mean grey matter thickness of V1, V2 and V3 (F(1,29)=.016, p=.901, η2=.052). As a main effect of visual area was seen, pairwise tests were conducted. The t-test showed V1 to be significantly thinner than V3 (p=.005), but not thinner than V2 (p=.094). There was no significant difference between V2 and V3 in thickness (p=.346) (see Figure 3.3). It is possible that the main effect shown in our ANOVA was driven by the difference between V1 and V3.

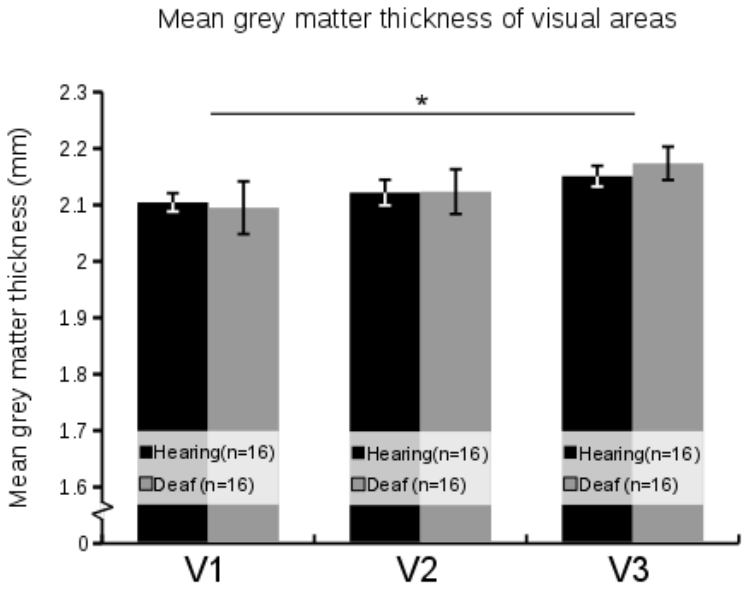

Figure 3.3 – A graph representing mean cortical thickness values of each visual area V1, V2 and V3 in the deaf and hearing groups. *=p<.05. Error bars represent 1+/- SEM.

3.6 Summary of Total Volume, Surface and Mean Thickness Results

No differences were seen between our deaf and hearing group in cortical volume, surface area or grey matter thickness within V1, V2 or V3. The total volume and surface area do not differ between groups in V1, however the main hypothesis in the current study was to test the cortical representation devoted to peripheral and central visual field processing, as these are the measures likely to show a difference between the congenitally deaf and hearing adults. Furthermore, even though the total volume and surface measures did differ in areas V2 and V3, the main aim was to investigate which eccentricity representations drive these differences. Separate regions representing the amount of cortex dedicated to processing the central (0-15 °), mid-peripheral (15-39 °) and far-peripheral (39-72 °) visual field extent within V1, V2 and V3 were defined. As done when comparing total volume, surface area and mean thickness, the measures extracted were: cortical volume (mm^3), surface area (mm^2), and thickness within the subdivisions of each visual area. The details outlining this analysis can be found in Chapter 2, Section 2.8.

3.7 Cortical Volume - Sub-divisions in V1, V2 and V3

3.7.1 V1 Sub-ROIs

To investigate the cortical volume of the three sub-ROIs within V1, a factorial mixed ANOVA was run, with a between subjects factor of group (deaf, hearing). There was no significant main effect of V1 sub-ROI volume ($F(2,60)=2.507$, $p=.090$, $\eta 2=.484$ (sphericity assumed $X^2(2) = 4.897$, $p=.086$; $\varepsilon= .845$). There was a significant interaction between V1 sub-ROI volume and group ($F(2,60)=5.299$, $p=.008$, $\eta 2=.819$), and no overall significant difference between groups ($F(1)=.024$, $p=.878$, $\eta 2=.001$). It was hypothesised that the visual field representations will differ between deaf and hearing participants. As a significant interaction was detected between ROI and group, further tests were conducted to investigate where these differences between groups were apparent.

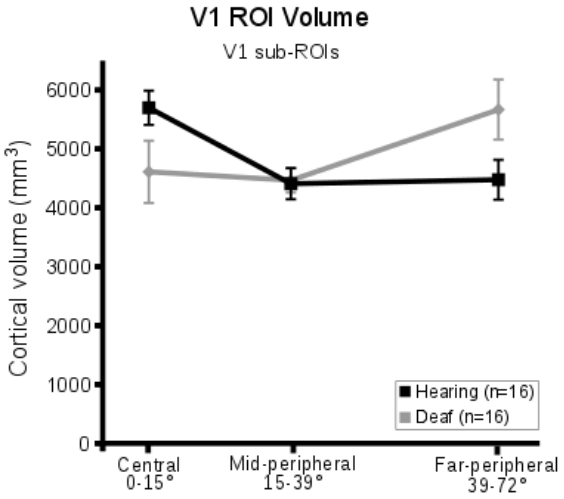

Figure 3.4 – A graph representing mean cortical volume values of each subregion of visual area V1, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

The t-tests showed a non-significant difference between our hearing and deaf participants, within the Central V1 sub-ROI, $t(30)=-1.806$, $p=.081$, Mid-peripheral sub-ROI ($t(30)= .170$, $p=.866$) and Far-peripheral sub-ROI ($t(30)= 1.949$, $p=.061$). Equal variances were assumed across all sub-ROIs (V1C: $F=1.880$, $p=.181$; V1M: $F=.845$, $p=.365$, V1P: $F=1.301$, $p=.263$) (see Figure 3.4). The results suggest that the cortical volume dedicated to processing the central and far-peripheral visual field is distributed differently

between deaf and hearing participants. The deaf individuals show a trend towards a larger amount of cortical volume devoted to processing the far-periphery, at the cost of a smaller volume dedicated to the central field, while in comparison the hearing showed the opposite effect.

3.7.2 V2 Sub-ROIs

V2 sub-ROI volume was compared in the same manner, using a factorial mixed ANOVA, with a between subjects factors of group (hearing, deaf). The assumption of sphericity was violated, ($X^2(2) = 7.248$, p=.027; $\varepsilon = .772$) and a Greenhouse- Geisser correction used. The ANOVA showed a significant main effect of V2 sub-ROI volume (F(1.629,47.229) =7.145, p=.003, $\eta 2$=.873). There was no significant interaction between V2 sub-ROI volume and group (F(1.629,47.229)=1.785, p=.184, $\eta 2$=.321). The between subjects effects test showed an overall significant difference between hearing and deaf groups, V2 sub-ROI volume, (F(1)=4.791, p=.037, $\eta 2$=.142).

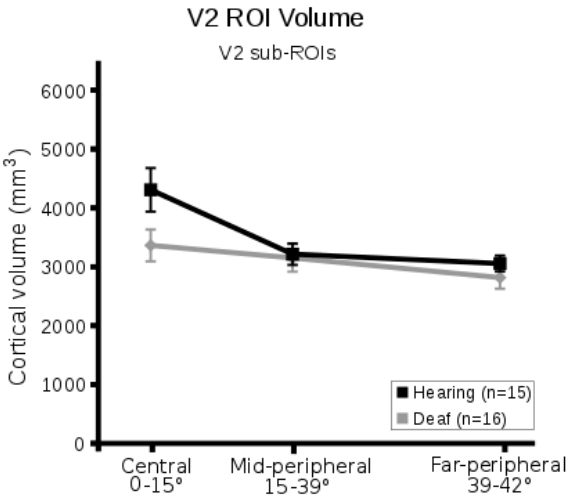

Figure 3.5 – A graph representing mean cortical volume values of each subregion of visual area V2, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

As a main effect of ROI in all of our participants, pairwise comparisons were conducted between sub-ROIs which showed the Central ROI to be significantly larger in volume than the Far-peripheral V2 ROIs (p=.005), whilst there were no significant differences between the Central and Mid-peripheral ROI (p=.087), nor between the Mid-peripheral and Far-

peripheral ROI (p=.547). As outlined in the V1 sub-ROI results, it was hypothesised that possible visual field representation differences between deaf and hearing could also include visual areas following V1. The ANOVA did however not show a significant interaction between volume and group, indicating no group differences in any V2 sub-ROI volumes. An overall effect between groups was indicated by a significant between-subjects test, where the overall volume of V2 differs between the groups.

3.7.3 V3 Sub-ROIs

A factorial mixed ANOVA, with a between subjects factors of group (hearing, deaf) was used to investigate the V3 sub-ROI volume data. Sphericity was not assumed for the V3 sub-ROI volume data ($X^2(2) = 8.069$, p=.018; $\varepsilon = .750$). The test showed a significant main effect of V3 sub-ROI volume, F(1.600,46.386)=10.434, p<.001, $\eta 2$=.963 and no interaction between V3 sub-ROI volume and group, F(1.600,46.386)=.131, p=.832, $\eta 2$=.067. A significant between subject effect was seen in the overall volumes of V3 sub-ROIs, F(1)=6.903, p=.014, $\eta 2$=.192.

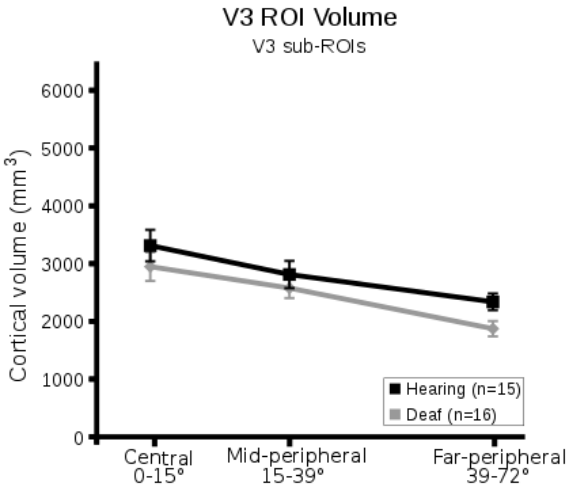

Figure 3.6 – A graph representing mean cortical volume values of each subregion of visual area V3, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

As there was a main effect of sub-ROI, pairwise comparisons were used. There was no significant difference between the Central and Mid-peripheral sub-ROI volume (p=.360). The Central ROI was significantly larger than the Far-peripheral sub-ROI (p<.001). The

Mid-Peripheral ROI was also significantly larger than the Far-peripheral sub-ROI (p=.006) in all participants. The results indicate that there are no differences in volume between the deaf and hearing individuals in any of the V3 sub-ROIs. There is an overall difference of volume, where the deaf show less volume in V3.

3.8 Cortical Surface Area - Sub-divisions in V1, V2 and V3

The volume measure extracted consists of both the cortical surface area and cortical grey matter thickness. The following tests were conducted on the surface area measures with a factorial mixed ANOVA, with a between subjects factors of group (hearing, deaf), and shows weather the driving factor behind the differences seen in the volume measures is driven by cortical surface area, or cortical thickness.

3.8.1 V1 Sub-ROIs

A factorial mixed ANOVA, with a between subjects factors of group (hearing, deaf) was performed to investigate V1 sub-ROI surface area. Sphericity was assumed for this data, ($X^2(2) = 2.079$, p=.354; ε= .935). The ANOVA showed a significant main effect of V1 ROI surface areas (F(2,60)=5.895, p=.005, η2=.860). There was also a significant interaction between the V1 ROI surface areas and group (F(2,60)=5.165, p=.009, η2=.808). Tests of between subjects effects showed no significant overall difference between groups in V1 sub-ROI surface areas (F(1,30)=.216, p=.645, η2=.074).

To further investigate the main effect of V1 sub-ROI surface area in all participants, pair-wise comparisons showed no significant difference between the Central and Mid-peripheral (p=.247), or Central and Far-peripheral sub-ROIs (p=.286). The Far-peripheral sub-ROI was significantly larger than the Mid-peripheral ROI (p=.007). It was hypothesised that possible visual field representation differences between deaf and hearing will be apparent once different eccentricities are considered. As the interaction between V1 sub-ROI surface area and group was significant, t-tests were carried out between the groups in each subregion of V1. The Far-peripheral ROI was significantly larger in the deaf compared to hearing participants (t(30)= 2.195, p=.036). There was no significant difference between groups within the Central (t(30)=-1.993, p=.055) and Mid-peripheral ROIs (t(30)= .474,

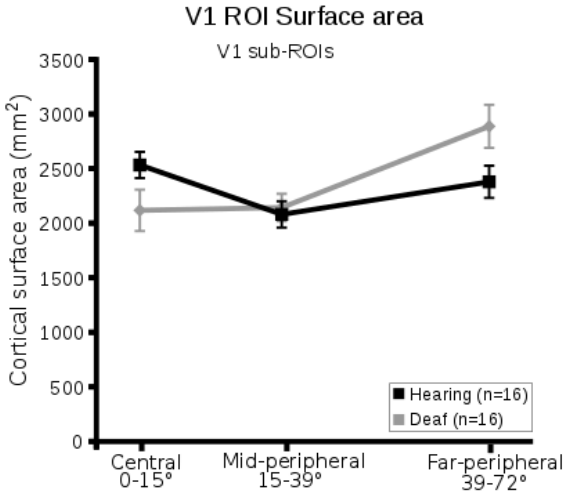

Figure 3.7 – A graph representing mean values of cortical surface area in each subregion of visual area V1, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

p=.639). Equal variances were assumed across all sub-ROIs (Central F=1.538, p=.225; Mid-peripheral, F=.001, p=.99; Far-peripheral ROI, F=1.327, p=.258) (see Figure 3.7). The cortical distribution differs significantly between deaf and hearing individuals within the cortical surface area representing the far-peripheral visual field. This appears to be at a cost of a smaller representation of the central visual field in the deaf, where the difference between groups is near significant.

3.8.2 V2 Sub-ROIs

The V2 sub-ROI surface area measure was investigated by using a factorial mixed ANOVA, with a between subject factor of group (hearing, deaf). Sphericity was assumed ($X^2(2) = 4.273$, p=.118; $\varepsilon = .858$). There was a main effect of V2 sub-ROI surface area, F(2,58)= 13.099, p<.001, $\eta 2$=.996, and no interaction between the sub-ROI surface area and group (F(2,58)=1.962, p=.150, $\eta 2$=.390). A test measuring between subjects effects showed no overall differences in V2 surface area between groups (F(1,29)=2.754, p=.108, $\eta 2$=.361). Pairwise comparisons revealed that the Central ROI was significantly larger than the Mid-peripheral (p=.038), and larger than the Far-peripheral ROI (p<.001). There were no significant differences in surface area between the Mid-peripheral and Far-peripheral ROIs (p=.058). The lack of interaction between surface area and group here indicates

that there are no differences between the deaf and hearing individuals in any of the V2 sub-ROIs.

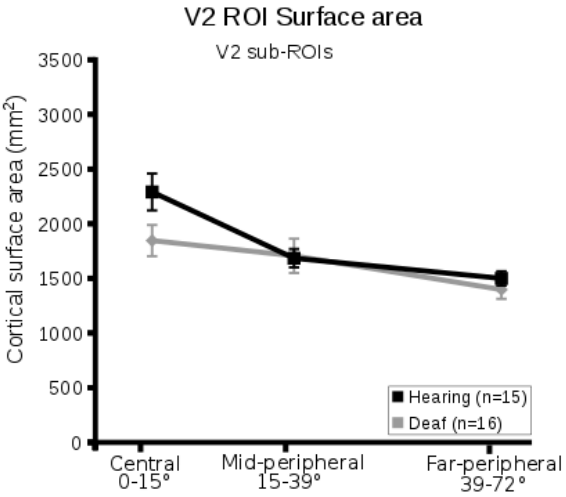

Figure 3.8 – A graph representing mean values of cortical surface area in each subregion of visual area V2, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

3.8.3 V3 Sub-ROIs

A factorial mixed ANOVA, with a between subjects factor of group (hearing, deaf) was used to investigate differences in the V3 sub-ROI surface areas. Firstly, sphericity of the data could not be assumed ($X^2(2) = 9.480$, p=.009; $\varepsilon = .777$). The test showed a significant main effect of V3 sub-ROI surface area (F(1.554,45.059)= 14.024, p<.001, $\eta 2$=.991). There was no significant interaction between the sub-ROI surface area and group (F(1.554,45.059)=.144, p=.814, $\eta 2$=.069). A significant difference was observed between subjects in V3 sub-ROI surface areas (F(1,29)=6.353, p=.017, $\eta 2$=.683). Pairwise comparisons in all subjects showed the Central ROI was not significantly different from the Mid-peripheral ROI (p=.070). The Far-peripheral ROI was significantly smaller than the Central ROI (p<.001) and Mid-peripheral ROI (p=.014) (see Figure 3.9). There was no interaction present between surface area and group here indicates that there are no differences between the deaf and hearing individuals in any of the V3 sub-ROIs.

The results indicate no significant differences between deaf and hearing participants in cortical surface area within any of the V3 subregions. There is an overall difference of

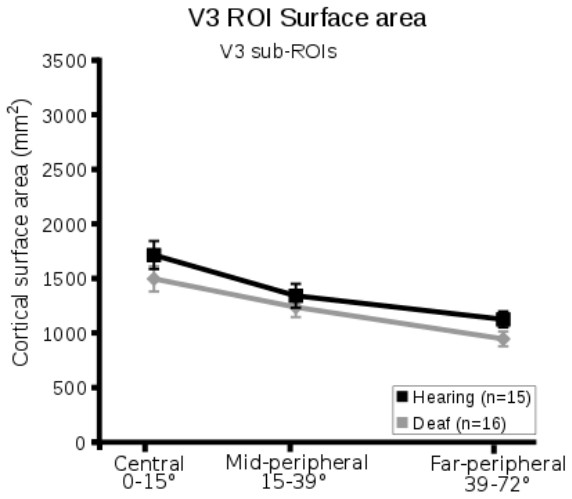

Figure 3.9 – A graph representing mean values of cortical surface area in each subregion of visual area V3, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

cortical surface area, where the deaf show less surface area combined in V3, as seen in the volumetric measure (see section V3 sub-ROIs–cortical volume).

3.9 Grey Matter Thickness - Sub-divisions in V1, V2 and V3

3.9.1 V1 Sub-ROIs

Differences in V1 sub-ROI cortical thickness across all participants and between groups were investigated with a factorial mixed ANOVA, with a between subjects factor of group (deaf, hearing). Mauchly's test of sphericity was not violated, $X^2(2) = 8.675$, p=.013; ε= .795. A main effect of V1 ROI thickness was present, F(1.589,47.674)=14.145, p<.001, η2=.992. There was no significant interaction between Group and ROI, F(1.589,47.674)=.923, p=.384, η2=.183. The between subjects effect test showed no overall significant differences in cortical thickness within the ROIs, F(1,30)=.037, p=.849, η2=.054. To follow up the main effect of ROI in all participants, pairwise comparisons were conducted across all participants (see Figure 3.10). No significant difference in cortical thickness between the Central and Mid-peripheral ROI (p=.122) was observed. The Central ROI was signifi-

cantly thicker than the Far-peripheral ROI (p<.001), and the Mid-peripheral ROI was significantly thicker than the Far- peripheral ROI (p<.001). The results indicate no differences in cortical thickness between groups in V1 subregions.

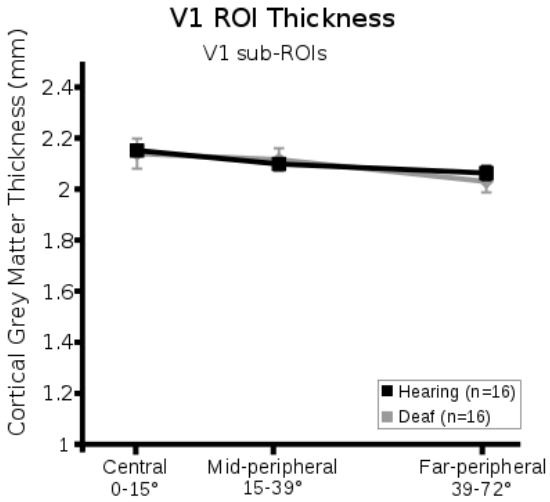

Figure 3.10 – A graph representing mean values of cortical thickness in each subregion of visual area V1, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

3.9.2 V2 Sub-ROIs

V2 sub-ROI grey matter thickness across all participants and between groups was investigated with a factorial mixed ANOVA, with a between subjects factor of group (hearing, deaf). Mauchly's test of sphericity was not violated for the V2 sub-ROI cortical thickness data ($X^2(2) = 2.621$, p=.270; $\varepsilon = .920$). A main effect of V2 sub-ROI was present, F(2,60)=12.140, p<.001, $\eta 2$=.994. There was no significant interaction seen between our groups and V2 sub-ROI thickness, F(2,60)=.175, p=.840, $\eta 2$=.076. No overall effect of Group was seen, F(1,30)=.001, p=.972, $\eta 2$=.050, when conducting a test for between subjects effects. To investigate the main effect of sub-ROI in all participants, pairwise comparisons were conducted (see Figure 3.11). These showed no significant difference in thickness between the Central and Mid-peripheral ROI, p=.056. The Far-peripheral ROI thickness was significantly greater than that of the Mid-peripheral ROI (p=.025) and the Central ROI (p<.001). There were no group differences in grey matter thickness in any V2 subregions.

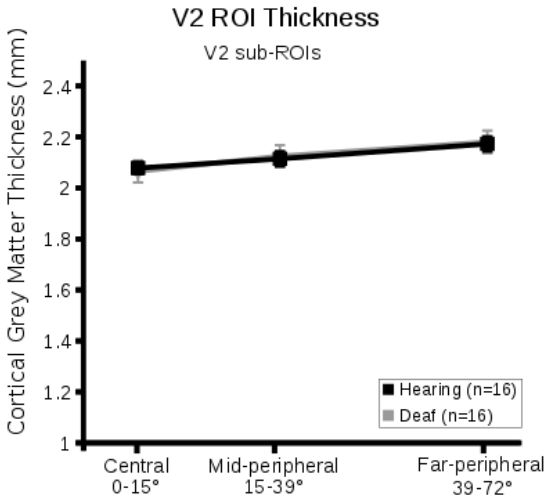

Figure 3.11 – A graph representing mean values of cortical thickness in each subregion of visual area V2, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

3.9.3 V3 Sub-ROIs

Cortical thickness in V3 sub-ROIs was explored across all participants and between groups, with a factorial mixed ANOVA, with a between subjects factor of group (hearing, deaf). Mauchly's test of sphericity was violated, ($X^2(2) = 6.619$, p=.037; $\varepsilon = .831$), and the Greenhouse- Geisser correction was applied. As with V1 and V2, a main effect of V3 sub-ROI thickness was apparent, F(1.661,49.831)=7.724, p=.002, $\eta 2$=.903, and no significant interaction between ROI thickness and group, F(1.661,49.831)= 1.142, p=.319, $\eta 2$=.222. There were no differences between subjects effects in this data, F(1,30)=.427, p=.519, $\eta 2$=.097. To investigate the main effect of sub-ROI in all participants, pairwise comparisons were conducted across all participants (see Figure 3.12). The Central ROI was significantly thinner than the Mid-peripheral ROI (p<.001) as well as Far-peripheral ROI (p=.009). No significant differences were seen between the Mid-peripheral and Far-peripheral ROIs (p=1).

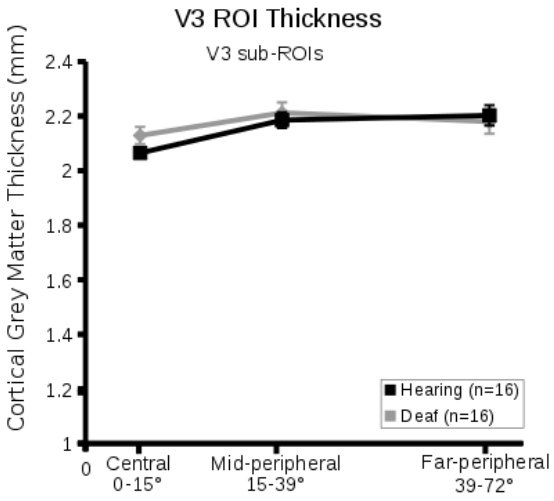

Figure 3.12 – A graph representing mean values of cortical thickness in each subregion of visual area V3, divided into three eccentricities, Central, Mid-peripheral and Far-peripheral, presented for the deaf and hearing groups. Error bars represent 1+/- SEM.

3.10 The cortical magnification factor

Extracting cortical magnification functions provide a way of quantifying the visual field extent in relation to the amount of cortical surface area dedicated to it in the brain ($mm^2/degrees^2$)(Cowey and Rolls, 1974). It provides a continuous variable within each visual area, as the subdivisions are not independent. The functions were extracted from each subregion of areas V1, V2 and V3. The three values extracted from the sub-ROIs of each visual area were used to fit a linear regression, where the gradient of this regression line was retrieved for each participant and the group means compared (for more analysis details see Methods, section 2.9). The cortical magnification gradients of each visual area were explored across all participants and between groups, with a factorial mixed ANOVA, with a between subjects factor of group (hearing, deaf). The ANOVA showed a main effect of the cortical magnification gradient between visual areas, $F(1.554,45.077)=38.185$, $p<.001$, $\eta 2=.568$. The interaction between these gradients in visual areas and group was also significant, $F(1.554, 45.077)=5.558$, $p=.012$, $\eta 2=.161$. As there was a main effect of visual area, pairwise comparisons including all participants showed that gradients of V1 were significantly shallower from V2 ($p<.001$) as well as V3 ($p<.001$). V2 gradients were also significantly shallower than V3 gradients.

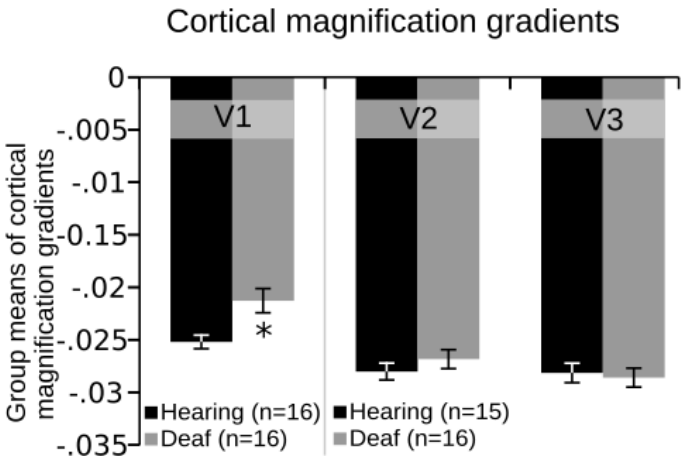

Figure 3.13 – A graph representing mean values of cortical magnification gradients in each visual area V1, V2 and V3, presented for the deaf and hearing groups. *=p<.05. Error bars represent 1+/- SEM.

As an interaction was significant between cortical magnification gradients of visual regions and group, t-tests comparing group means were conducted. These t-tests, when corrected for multiple comparisons, showed a significant difference in V1 gradients between the deaf and hearing participants, t(30)=2.966, p=.006. There was no significant difference between these gradients in either V2 or V3 (V2: t(29)=.975, p=.338; V3: t(29)=-.345, p=.733). Equal variances were assumed within all three areas (V1: F=2.346, p=.136, V2: F=.954, p=.337, V3: F=.004, p=.950; see Figure 3.13). The results clearly showcase the cortical distribution differences seen in both the volume and surface area measures of V1 subregions. A shallower gradient in deaf individuals indicates relatively less cortical surface area dedicated to the central visual field and more dedicated to the far-periphery, relative to hearing controls.

3.11 Discussion

3.11.1 Summary of Key Results

The experiments described aimed to determine if the influence of lifelong auditory deprivation can lead to plasticity within early visual cortex. The study measured the amount of cortex in visual areas V1, V2 and V3 devoted to processing the visual field, extending to the far-periphery, in congenitally deaf and hearing adults. A significant difference was

observed between deaf and hearing participants in the distribution of cortex relative to visual eccentricity. Deaf participants showed a larger cortical surface representation of the far-peripheral visual field and smaller central visual field representation in V1, but not V2 and V3, when compared to hearing controls. This effect is seen in the measure of cortical volume, and is driven by differences in cortical surface area, not cortical thickness.

3.11.2 Overall volume, surface area and cortical thickness results

The measures of the total cortical volume, surface area and mean thickness of areas V1, V2 and V3 were extracted. The data showed no significant differences in total overall volume, surface area or mean cortical thickness in V1 between deaf and hearing participants. The volume and surface area of visual area V3 is significantly smaller within deaf participants compared to hearing participants, whilst the cortical thickness measure showed no differences. The results also showed that in the deaf group V2 was smaller in volume but not surface area, when compared to the hearing group. The results presented here add to previous studies investigating intramodal plasticity in deaf visual cortex, showing a significant effect of plasticity in V1. This finding helps clarify the current stance, as there are a number of studies report various different effects of plasticity, with no clear concensus. Allen et al. (2013) showed the total volume of the calcarine sulcus to be larger in deaf than hearing individuals, whilst Fine et al. (2005) investigated visual areas V1, V2, V3, V4 and V5 and found no significant differences in overall surface area of the mentioned visual areas. Smittenaar et al. (2016) reported thinner grey matter within V1 of deaf individuals. The results of previous studies are restricted due to the smaller extent of V1 investigated, where the far-peripheral representation of V1 is not included (Fine et al., 2005; Smittenaar et al., 2016). These results mentioned are restricted by methodological aspects of visual field mapping in fMRI, as only a limited field of view is available within typical visual displays in most scanners (from 15-37.5 °). This makes it difficult for these studies to identify possible neural substrates of heightened visual performance in the far-periphery. Using a novel visual stimulus delivery method extendeding to 72 ° in each hemifield, this study was able to include the far peripheral visual field within which the greatest behavioural advantages in deaf individuals have previously been detected (Buckley et al., 2010; Lomber et al., 2010). The novel finding described here is the difference in the relative cortical surface distribution in V1 of deaf individuals.

3.11.3 SubROI results

It was hypothesised that the relative distribution of cortex devoted to peripheral and central visual field processing will show differences due to plasticity in congenitally deaf participants when compared to hearing controls. The amount of cortex was divided into comparable sections dedicated to processing the Central (0-15 °), Mid-peripheral (15-39 °) and Far-peripheral (39-72 °) visual field extent within V1, V2 and V3. The results include measurements of cortical volume (mm^3) surface area (mm^2) and thickness (mm) within the subdivisions of each visual area.

3.11.4 Cortical Volume- subROIs

The Central V1 ROI in deaf participants is significantly smaller in volume than in hearing, and the Far-peripheral region is significantly larger in the deaf. As the overall volume of area V1 does not differ between the groups, it is the distribution of cortex relative to eccentricity which is affected by deafness. This result suggests that the emphasis of the far-periphery in deaf primary visual cortex comes at the cost of a smaller cortical representation of the central visual field. The emphasis of the far-periphery seen in V1 is not apparent in area V2. There was however a significant difference between the groups within the volume of Central V2 ROI, showing a lower surface area in the deaf, compared to hearing. There was no significant difference within the Far-peripheral representation within V2. In area V3, there was an overall difference in cortical volume, across all participants; when comparing subdivisions of the regions, the cortical volume decreases with eccentricity.

3.11.5 Cortical Surface Area

The surface area measure shows the same pattern of cortical distribution in V1 as seen in the volumetric measure. When comparing the means within the Far-peripheral ROI between groups, the deaf have a significantly larger surface area devoted to the far periphery compared to the hearing group. The Central ROI on the other hand, shows a trend towards the deaf participants having less cortical surface devoted to this representation. The overall surface area of V2 does not differ between the two groups, however

there was a trend towards a smaller cortical surface area in the deaf within the Central ROI. Deaf individuals show a significantly smaller total cortical surface area in V3, when compared to the hearing participants, and this effect was not specific to any of the sub-regions within V3. These differences in V1, V2 and V3 of deaf individuals are novel and have, to our knowledge, never been presented before. Song et al. (2015) suggest that the two dimensions measuring cortical volume, namely thickness and surface area, contribute differently to processing advantages. A thinner cortex with larger surface area is perceptually advantageous. Our findings incorporate a much larger portion of the visual field than shown before, and the results do not show thinner cortex in early visual areas of deaf individuals. This could suggest that it is an increase in cortical surface area rather than cortical thickness which facilitates behavioural visual processing advantages seen in the deaf population. Alongside this result, larger receptive fields encoding the periphery in V1 have been found by (Smittenaar et al., 2016). As the researchers suggest in their paper, an enhancement in resolution with smaller receptive fields in V1 would need to be met with cortical expansion to maintain higher visual sensitivity. Indeed, the results show a larger cortical surface area dedicated to the far-periphery and this is possibly met with smaller receptive fields in deaf individuals when compared to hearing controls.

3.11.6 Cortical Magnification

The deaf participants had a significantly shallower cortical magnification gradient compared to hearing controls in V1, but not V2 and V3. The shallower gradient indicates a higher cortical emphasis within the peripheral visual field, whilst hearing participants showed a steeper gradient,indicating a relatively larger cortical emphasis devoted to the central, and less to the peripheral visual field, compared to deaf participants. In agreement with the set out hypothesis, a larger representations of the far-periphery relative to central visual field was found in V1 of deaf individuals. This provides novel evidence indicating that the cortical surface area devoted to the visual field representation differs in the primary visual cortex of deaf compared to hearing adults.

3.11.7 Larger peripheral representations and visual performance

The proportionally larger representation of the far-periphery in deaf individuals provides a possible explanation to behavioural evidence of heightened visual field sensitivity observed at both near (30 °) and far peripheral (60 °) kinetic perimetry measurements (Buckley et al., 2010, Stevens and Neville, 2006). This link can be tested in the future by comparing cortical representations with behavioural performance in a peripheral visual task within individuals. Effects of higher sensitivity in the visual periphery in this study emerge well beyond the field of view used for sign language (7 °, Bosworth et al., 2000). Therefore, the use of a visuo-spatial language cannot explain the heightened sensitivity in the far-peripheral visual field, especially beyond 60 °. It is more plausible that this behavioural advantages emerge in order to compensate for the lack of auditory cues or stimuli which would otherwise direct a hearing individual to events in the far-periphery or even outside of the visual field. Future studies incorporating either response times or speed of orienting to visual targets or stimuli changes across the visual field could elucidate this further. An experiment incorporating a design in virtual reality could test the entire visual field and could further explore the far-peripheral advantage in a more naturalistic environment.

3.11.8 Grey Matter Thickness

Differences in cortical thickness are also predictive of cortical plasticity. For example, Voss and Zatorre (2012) showed that plasticity as measured by cortical thickness within the occipital cortex of blind individuals predicted their performance in auditory tasks. Cortical thickness can vary over threefold across different cortical locations within the same cortical regions within one individual (Fischl et al., 1999). This study therefore investigated the mean cortical thickness across ROIs within visual areas V1, V2 and V3 as well as the sub-regions within each of these areas, and found no significant differences in thickness between deaf and hearing participants. There is evidence to suggest deaf individuals have a thinner cortical layer in V1 (Smittenaar et al., 2016), in which the study used a definition of V1 reaching out to 37.5 ° to measure cortical thickness. They showed no systematic relationship between eccentricity and thickness. Our results reach beyond previously investigated regions, measuring at further eccentricities, where visual processing advantages have been shown (Buckley et al., 2010), but still found no difference

between groups. The differences observed in cortical thickness can also be explained by anatomical variation as to the location of V2 and V3 on the cortical surface. The calcarine sulcus, which contains V1, is thinner and contains many sulci. Areas V2 and V3 however are located outside of this sulcus, where the sulci are less convoluted and allow for better anatomical segmentation which helps extract the cortical thickness measure. Along with anatomical factors, it is also important to consider the limitations of our measures and the restricted resolution of cortical thickness. In the human cortex, grey matter thickness can vary between 1-4.5 mm, with a between subject standard deviation of 0.5mm (Fischl et al., 1999). As the voxels sampled are $1mm^3$ in size, the present measure is only accurate to the nearest 0.5mm. Cortical thickness extraction also benefits highly from surface-based averaging which aligns cortical folding patterns (Fischl et al., 1999), as the crowns of gyri showed an average thickness of 2.7 +/- 0.3mm compared to the sulcal fundi, 2.2 +/- 0.3mm (Fischl and Dale, 2000). The calcarine sulcus, where V1 is located, is heavily convoluted, therefore requiring precise measurement. Our measurements are fairly coarse, and is therefore suboptimal for precise measurement and curvature analysis is beyond the scope of the current study. The current results are however based on manual grey and white matter segmentations, which vastly improve on automatic segmentations most commonly used across the literature. Future investigations of cortical thickness differences in deaf individuals would be further improvement by using structural MRI protocols designed especially to extract grey matter thickness. These include protocols such as those used by Glasser and Van Essen (2011). The researchers retrieve a better contrast for myelin by increasing the contrast to noise ratio by using T1 and T2 weighted scans to eliminate image intensity biases which arise in these images. These protocols would help reduce the influence of possible confounds introduced by the limitation of our sample resolution, especially due to cortical thickness only varying between 1-4.5 mm. Higher resolution MRI structural sequences could also allow for a better estimate of cortical thickness.

3.11.9 Limitations of volume and cortical surface measures

It is possible that the study did not detect overall size differences in early visual areas of our sample as the size of early visual areas can vary threefold between healthy individuals (Andrews et al., 1997; Dougherty et al., 2003; Duncan and Boynton, 2003). No overall size differences were seen in V1 between groups, but there was a significant difference in the

distribution of the representation of eccentricity across cortex. Increased representations of the far-periphery are not simply a reflection of total surface area differences in V1, but the differences in distribution of cortex between central and peripheral processing in deaf individuals, when compared to hearing controls. The definitions of V2 and V3 are also prone to more error in the current study. The wide-field stimulus presentation used to extend into the far-periphery compromises the rotating wedge stimulus, where it only extends to ca. 20 ° along the vertical meridian. As V1 has a full hemifield representation, and its definition is highly guided by the anatomy of the calcarine sulcus (Benson et al., 2012), it is much easier to define compared to the upper and lower quaterfield representations of V2 and V3. Due to this, the definitions of V2 and V3 in this study are subject to higher error compared to V1. In order to strengthen these results, a method able to stimulate further into the vertical meridian would be beneficial, as well as several retinotopic scans which could be averaged for clearer results. A possible source of variability in our data could have been due to unstable fixation, which reduce the quality of the identification of visual maps, as it was not monitored in the scanner. However, a previous study has noted that deaf individuals are better at maintaining fixation than their hearing controls (Buckley et al., 2010). A larger proportion of our participants had their heads tilted (3 °) in the scanner towards the fixation cross, as it was placed at the edge of the screen to map each hemifield separately. All the data acquired suggests that our participants maintained stable fixation across long periods in time, as it was possible to accurately identify visual field maps (apart from one hemifield of a hearing participant, where V2 and V3 were not identifiable).

3.12 Conclusions

These data suggest that compensatory plasticity within the visual cortex as a consequence of auditory deprivation becomes apparent at large eccentricities. Previous research was not sensitive to this as the far-periphery was not stimulated within the fMRI experiments (Fine et al., 2005; Bavelier et al., 2001; Scott et al., 2014; Smittenaar, et al., 2016). Our results show evidence of plasticity within the cortical distribution of central and peripheral visual field representations within the primary visual cortex of congenitally deaf adults.

Chapter 4

Neural Responses in Motion Processing Areas of Deaf and Hearing Adults

4.1 Overview

Lifelong auditory deprivation can lead to visual processing advantages, particularly in visual motion processing. The current study investigated effects of plasticity within far-peripheral visual motion processing. fMRI activity to full-field coherent optic flow stimuli and incoherent motion extending to 72° was measured, in order to investigate neural substrates behind the far-peripheral visual motion advantage observed in deaf studies (Codina et al., 2017; Buckley et al., 2010; Lomber et al., 2010). The study focused the investigations on the well established motion area V5/MT+ (Tootell et al., 1995), as well as on V6, a visual area with a large peripheral representation and selectivity for visual motion (Galletti et al., 2001; Pitzalis et al., 2013). Alongside visual areas, signals were also measured in areas of the superior temporal cortex, including auditory regions, as evidence of cross-modal plasticity has also been found in the auditory cortex of deaf individuals (Karns et al., 2012; Scott et al., 2014; Fine et al., 2005). These neural regions were hypothesised to show differential activation to far-peripheral motion, therefore potentially being involved in heightened visual sensitivity.

4.2 Background

Advantages of deaf individuals within peripheral visual processing, such as motion detection and visual orienting, have been reported in several behavioural studies (Neville and Lawson, 1987; Loke and Song, 1991; Bavelier et al., 2000; Bosworth and Dobkins, 2002; Proksch and Bavelier, 2002; Stevens and Neville, 2006; Hauthal et al., 2013; Heimler and Pavani, 2014; Shiell et al., 2014; Codina et al., 2017). In congenitally deaf cats, Lomber et al. (2010) found the largest behavioural advantages in the far-periphery (beyond 60°). In deaf human adults, Buckley et al. (2010) and a recent study by Codina et al. (2017) found that deaf participants had the greatest visual advantages in the near- (ca. 30°) and far-periphery (>60°). However, the neural mechanisms supporting increased visual motion sensitivity are still not fully understood, as investigating motion perception with fMRI in far-peripheral visual fields poses methodological challenges. Some of these challenges are caused by the scanner bore limiting the extent of the visual field it is possible to stimulate, as discussed in section 2.4. Studies investigating cortical plasticity as a result of hearing loss have found mixed results a number do not show any differences between deaf and hearing individuals (Vachon et al., 2013; Fine et al., 2005), whilst others have found evidence of cortical reorganisation in the deaf brain. Importantly, these studies do not measure responses extending beyond 30° into the periphery (Bottari et al., 2012; Heimler and Pavani, 2014). It is crucial to investigate this portion of the visual field, as the largest behavioural advantages can be seen beyond 60° (Buckley et al., 2010; Lomber et al., 2010). Findings that demonstrate heightened sensitivity here can be explained using an ecological perspective. Auditory cues can be useful in directing hearing individuals to events in the far-periphery, or to those outside the visual field entirely. As deaf individuals lack this type of input, it is likely that they would benefit the most from higher visual sensitivity beyond 30°.

4.2.1 V5/MT+

Firstly, area V5/MT+ was investigated as a possible substrate of heightened visual motion sensitivity. V5/MT+ is a widely known visual motion area (Tootell et al., 1995), and has been investigated in deaf subjects with visual stimuli within a limited range of eccentricities. Several studies have investigated the region with peripheral stimuli, however

not extending beyond 45° into the visual field (Bavelier et al., 2000; Karns et al., 2012; Scott et al., 2014; Fine et al., 2005). Bavelier et al. (2000) observed a larger extent of activation in V5/MT+ of deaf participants, when compared to hearing, when attending to the peripheral condition (6.66-8°). Similarly, Scott et al. (2014) found larger recruitment of V5/MT+ in deaf individuals when responses of peripheral (11-15°) over central (2-7°) visual stimuli were contrasted. It is hypothesised that V5/MT+ will be recruited to a higher degree in deaf individuals when stimulating a larger extent of the visual field than previously. This is expected to be particularly pronounced in the far periphery, where increased visual sensitivity is likely to incur the greatest advantage in deaf individuals.

4.2.2 V6

Area V6 was also investigated, as this region is responsive to visual motion with a strong peripheral visual field processing bias (Pitzalis et al., 2013, 2010; Fattori et al., 2009b). V6 shows a strong preference for coherent motion processing, especially when this motion is egomotion compatible (Cardin and Smith, 2011, Cardin et al., 2012). Retinotopically, it shows a full representation of the contralateral hemifield (Pitzalis et al., 2006; Fattori et al., 2009a). It has not previously been investigated in deaf individuals, and serves as a potential substrate behind the increased peripheral sensitivity. Tracer studies in non-human primates show area V6 to have a number of reciprocal connections with visual areas, including to motion areas MT and MST, which are part of the MT+ motion region in primates and are homologous to the human motion area V5/MT+. This finding led Galletti et al. (2001) to believe that V6 is heavily involved in dorsal visual stream processing. Additionally, in human studies of visually evoked potentials, Pitzalis et al. (2013) have found parallel neural signals to coherent motion in both V6 and V5/MT+, implicating comparable roles in visual flow signal integration.

4.2.3 Auditory Cortex

Alongside visual motion processing areas, auditory cortex was also included as a possible region supporting visual processing advantages in deaf individuals. A number of studies in deaf individuals provide evidence of cross-modal activation of superior temporal regions, including auditory cortex, in visual processing (Vachon et al., 2013; Finney and Dobkins,

2001; Sadato et al., 2005). Fine et al. (2005) investigated a number of visual areas (V1 / V2 / V3 / V4 and V5/MT+) as well as auditory cortex. The auditory cortex of deaf individuals displayed higher activation compared to hearing when presented with near peripheral visual stimuli (10° diameter disk containing motion, centred 15° from fixation), giving evidence of functional remapping of auditory cortex in deaf individuals. Cross-modal processing involving visuo-somatosensory stimuli also show increased activation of the deaf auditory cortex (Karns et al., 2012). The superior temporal cortex, within which auditory cortex lies, also holds auditory associative regions that are multisensory in nature. For example, areas such as the Planum Temporale (PT) show higher activation during visual peripheral motion processing (Scott et al., 2014). Area PT is located posterior to primary auditory cortex, which is also known as Heschls gyrus. Furthermore, primate studies show interconnections between far-peripheral visual representations of visual cortex with auditory cortex (Falchier et al., 2002). It is therefore possible that similar connections in humans are present, and may be strengthened as a result of cross-modal plasticity, and show increased recruitment in motion processing. Although the recruitment of auditory cortex for visual tasks is quite well established in deaf individuals, it has not been studied with wide field stimulation, nor has it been divided into primary and secondary associative regions, in line with far-peripheral motion stimulation. All the aforementioned studies demonstrating various behavioural and neural findings generally do not investigate motion detection in the peripheral visual field beyond 30°. As behavioural advantages are seen in the far-periphery, the current study aimed to bridge this gap through wide-field motion stimulation in fMRI.

4.3 Summary and Hypotheses

The goal of the current study was to investigate plasticity within motion processing cortical areas in deaf individuals, compared to hearing controls. Based on behavioural studies showing advantages in the far-peripheral perception of visual stimuli (Buckley et al., 2010; Codina et al., 2011b), it was hypothesised that areas involved in visual motion processing in the far-periphery would show greater activation in deaf participants, compared to hearing. It was also hypothesised that effects of cross-modal plasticity will be apparent, in the shape of positive activation in the auditory cortex of deaf individuals. Specifically, regions which are located posterior and anterior to primary auditory cortex (HG), which are secondary

and more multisensory in nature, were expected to show higher modulation in congenitally deaf individuals. Conversely, the study expected to observe suppression in this area in hearing participants, when processing coherent visual motion.

4.4 Methods

4.4.1 Participants

The study included 40 subjects, of which 13 were congenitally and profoundly deaf individuals (mean age=32, range=20- 48 years, 5 females). 27 were hearing individuals (mean age=26, range=20-48 years, 14 females). There was no significant difference in age between the groups, where equal variances could not be assumed (Levene's test, $F(38)=13.9$, $p<.001$) with a corrected t statistic of $t(14.7)=2.03$, $p=.060$. All participants self reported normal or corrected-to-normal vision. Each deaf participant also filled out a brief questionnaire regarding age and aetiology of deafness (see Chapter 2, Table 2.1). All deaf participants reported severe to profound hearing loss in both ears (>70db) since birth or very early childhood. All participants gave their informed consent in accordance with the Declaration of Helsinki. The study was approved by The York Neuroimaging Centre Research Governance Committee (Department of Psychology, University of York).

4.4.2 Data Acquisition

Each participant underwent one or two separate scanning sessions, during which functional and structural MRI data were acquired using a 16 Channel Posterior Brain Array coil (Nova Medical) in a GE 3 Tesla Signa Excite HD scanner at the York Neuroimaging Centre. The structural data were acquired with high resolution T1-weighted structural isotropic scans. Functional data were acquired with a BOLD T2* EPI sequence. Alongside the functional scans, a proton density scan was also acquired in the same imaging plane as the functional data for all participants. This was used to aid the alignment of functional to structural data (further details are described in Chapter 2, Section 2.6).

4.4.3 Visual Motion Stimulus

The motion stimuli used in this paradigm aimed to maximally activate visual motion areas V5 and V6, with high contrast optic flow motion in depth stimuli presented in a blocked design (based on Cardin and Smith, 2011; Pitzalis et al., 2010, see Section 2.10). The motion stimuli were also used to investigate three divisions of auditory cortex. The block design was presented with Psykinematix (Beaudot, 2009) and included coherent and incoherent motion blocks, interleaved with a black fixation screen. All motion presented extended out to the far periphery 72° along the horizontal meridian and roughly 20° within the vertical plane, in each hemifield tested (further described in Chapter 2, Section 2.4).

4.4.4 Data Analysis

In the current study, several separate regions of interest (ROIs) were chosen to measure the response profile to visual optic flow motion stimuli. The BOLD percent signal change was taken as a proxy for the neural response of visual areas V5/MT+ and V6, as well as from three divisions within the superior temporal cortex: Te1.2, Heschl's Gyrus (HG) and Planum Temporale (PT). The V5/MT+ ROI was defined by combining three separate atlas definitions within FSL: a cytoarchitectonic definition of V5/MT+ by the Juelich Histological Atlas (Eickhoff et al., 2007) as well as functionally defined areas of TO1 and TO2 in a brain atlas created by Wang et al. (2015). For a full description of these methods see Chapter 2, Section 2.13.1. For area V6, a spherical ROI was created in each hemisphere. The centre of this sphere was identified based on a group mean activation cluster derived through contrasting the voxels responsive to coherent over incoherent motion condition blocks. The sphere was grown around the centre of gravity of this cluster, in both hemispheres, and transformed into each individual participant's structural space (See Chapter 2, Section 2.13.2 for more detail). Heschl's gyrus and Planum Temporale definitions were taken from the Harvard-Oxford Cortical Structural Atlas (Harvard Center for Morphometric Analysis) in FSL, and region Te1.2 from the Juelich histological atlas (Eickhoff et al., 2007) in FSL (for more detail see Chapter 2, Section 2.13.3). These three regions were chosen in order to separate the broader auditory area in the superior temporal cortex (along the Sylvian fissure), superior or inferior to Heschl's gyrus, to include regions rep-

resenting primary, secondary and associated auditory regions. These masks were chosen to investigate the PT and HG as it belongs to an accessible and established brain atlas (Harvard-Oxford Atlas) and the region has previously been used by a number of studies on cortical plasticity in deaf individuals (Fine et al., 2005; Cardin et al., 2016). Area Te1.2 has also been well established and used in a number of relevant studies (Karns et al., 2012; Bola et al., 2016). The dependent measure extracted from each ROI was the mean percentage signal change in the BOLD signal during the coherent and incoherent motion blocks relative to the black fixation screen. This was extracted using the Featquery tool within FSL (FMRIB toolbox).

4.5 Results

Neural activation evoked by motion stimuli within each ROI was statistically tested using a factorial mixed ANOVA with a between-subject factor of group (deaf, hearing) with IBMs SPSS 20. The age difference between the deaf and hearing groups included in this study was near significance (p=.060). A study by Billino et al. (2008) investigated the effect of age on visual processing, and indicates that visual motion perception is not equally prone to age-related decline. They found no correlations of age within radial motion, however did find negative correlations with biological and translational motion. Our experiment presents radial and angular optic flow motion in the coherent blocks, and random motion in the incoherent motion blocks. Based on the findings of Billino et al. (2008), these motion types are the least likely to be affected by the age range of participants. Possible age effects were, however, considered in the statistical analyses by including age as a covariate.

4.6 Visual Motion Areas

4.6.1 V5/MT+

To investigate possible activation differences in area V5/MT+, a factorial mixed ANOVA was conducted with factors of hemisphere (left, right) and motion type (coherent, incoherent), with a between subjects factor of group (deaf, hearing). Signals across hemispheres were investigated as previous studies have shown left lateralisation of activation in

V5/MT+ when processing motion stimuli in fMRI (Bavelier et al., 2001). Age was used as a covariate in the initial ANOVA to rule out effects of age upon the results of all participants. Age did not show any significant interactions with either hemisphere ($F(1,37)=.773$, $p=.385$, $\eta 2=.020$) or motion type ($F(1,37)=.143$, $p=.707$, $\eta 2=.004$). A second ANOVA was therefore conducted, without including age as a covariate (See Figure 4.1. Firstly, a test of between subjects effects showed no significant overall difference between the deaf and hearing subjects in V5/MT+ activation, $F(1,38)=1.562$, $p=.219$, $\eta 2=.039$. There was no significant main effect of hemisphere in V5/MT+ activation ($F(1,38)=1.029$, $p=0.317$, $\eta 2=0.026$). There was no interaction between hemisphere and group ($F(1,38)=0.687$, $p=0.412$, $\eta 2=0.018$). There was a significant main effect of motion type ($F(1,38)=90.361$, $p<.001$, $\eta 2=0.704$), however there was no significant interaction between the motion type and group ($F(1,38)=0.004$, $p=0.95$, $\eta 2=0$). There was also a significant interaction in all participants between hemisphere and motion type ($F(1,38)=15.162$, $p<.001$, $\eta 2=0.285$).

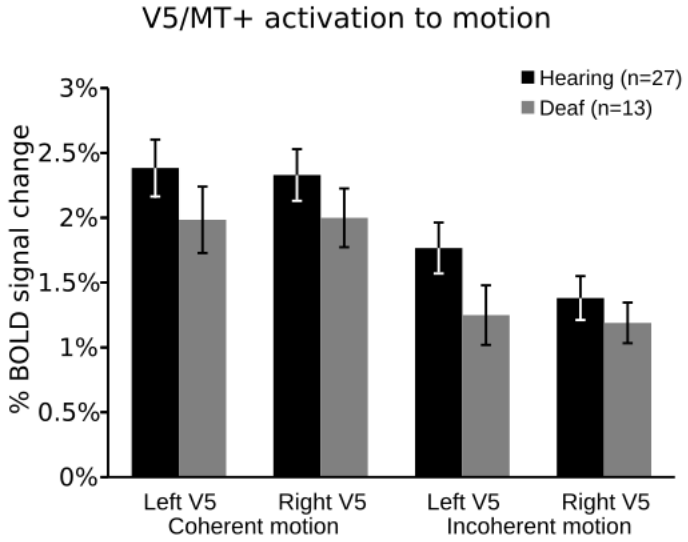

Figure 4.1 – A graph representing mean values of percent signal change in visual motion area V5/MT+, divided into hemispheres and motion type, for the deaf and hearing groups. Error bars represent +/-1 SEM.

This interaction is likely to be driven by the main effect of motion type in V5/MT+. Overall the study found higher activation to coherent than incoherent motion across participants but no main effect of hemisphere.

4.6.2 V6

To investigate possible activation differences in area V6, a factorial mixed ANOVA was conducted, with factors of visual hemifield viewed (contralateral, ipsilateral) and motion type (coherent, incoherent) with a between subjects factor of group (deaf, hearing). Percent signal change of the ipsilateral and contralateral V6 ROI was averaged, as previous studies using wide-field retinotopy show a full contralateral hemifield representation in V6 (Pitzalis et al., 2006). Age was used as a covariate in the initial ANOVA to rule out effects of age upon the results of all participants. Age did not show any significant interactions with either visual hemifield viewed ($F(1,37)=2.497$, $p=.123$, $\eta 2=.063$) or motion type ($F(1,37)=.192$, $p=.664$, $\eta 2=.005$).

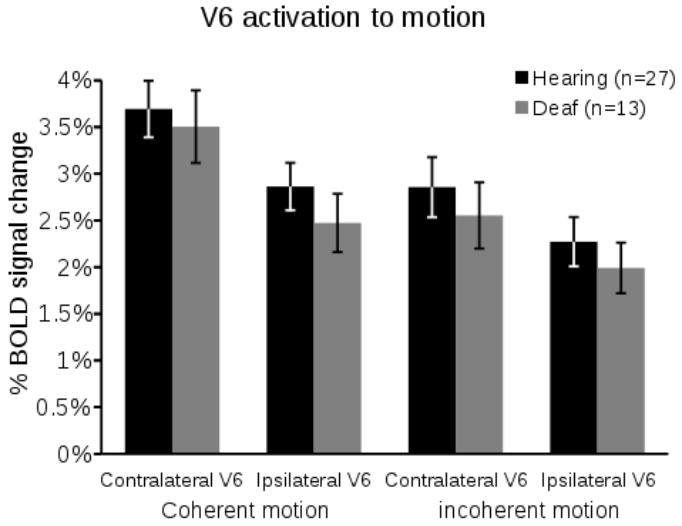

Figure 4.2 – A graph representing mean values of percent signal change in visual motion area V6, divided into view and motion type, for the deaf and hearing groups. Error bars represent +/-1 SEM.

A second ANOVA was therefore conducted, without including age as a covariate (See Figure 4.2). It was hypothesised that V6 activation would be higher in deaf individuals, as it has a large emphasis in processing peripheral motion. A test of between subjects effects showed no significant difference between the deaf and hearing subjects, $F(1,38)=.426$, $p=.518$, $\eta 2=.011$. There was a significant effect of visual hemifield viewed in V6 activation, ($F(1,38)=31.636$, $p<.001$, $\eta 2=.454$) however this did not interact with the factor of group ($F(1,38)=.111$, $p=.741$, $\eta 2=.003$) . There was also a main effect of motion type ($F(1,38)=72.037$, $p<.001$, $\eta 2=.655$), but no interaction between motion type and group ($F(1,38)=.000$, $p=.989$, $\eta 2=.000$). There was also a significant interaction between visual

hemifield viewed and motion type ($F(1,38)=17.615$, $p<.001$, $\eta 2=.317$).

As main effects of visual hemifield viewed and motion type were apparent, pairwise comparisons were conducted to establish where the effect was most prominent. Activation to motion type showed a significant difference between the contralateral and ipsilateral V6 when viewing coherent motion ($t(39)=7.021$, $p<.001$) and incoherent motion ($t(39)=4.349$, $p<.001$). When comparing coherent and incoherent motion activation within each hemifield stimulated, there was a significant difference in the ipsilateral view ($t(39)=6.591$, $p<.001$) as well as contralateral view ($t(39)=9.612$, $p<.001$), where activation was higher in the contralateral view compared to ipsilateral, and in both of these conditions coherent motion elicited the higher response. The results showed V6 activation to be higher within the contralateral hemisphere, and to coherent motion. These results support previous studies (Pitzalis et al., 2006; Fattori et al., 2009b), which demonstrated that V6 prefers coherent optic flow fields, compatible with egomotion (Cardin and Smith, 2011; Cardin et al., 2012b).

4.7 Auditory Cortex

To explore the nature of cross-modal plasticity in deaf adults, activation was compared across all three auditory regions identified within the superior temporal cortex (STC). Further, effects of lateralisation were also investigated, as earlier studies have shown functional differences in the activation of right and left regions of the STC between deaf and hearing participants (Finney and Dobkins, 2001; Scott et al., 2014). Higher modulation was expected in multisensory regions of the STC in deaf individuals to coherent wide-field motion, compared to incoherent wide-field motion.

4.7.1 Te1.2

To investigate possible activation differences in the anterior auditory region of Te1.2, a factorial mixed ANOVA was conducted, with factors of hemisphere (left, right) and motion type (coherent, incoherent), as well as a between subjects factor of group (deaf, hearing). Age was used as a covariate in the initial ANOVA to rule out effects of age upon the results of all participants. Age did not show any significant interactions with either hemisphere

(F(1,37)=.134, p=.716, η2=.004) or motion type (F(1,37)=.025, p=.874, η2=.001). A second ANOVA was therefore conducted, without including age as a covariate (See Figure 4.3). Test of between subjects effects showed an overall significant difference between the deaf and hearing group, (F(1)=10.110, p=.003, η2=.210). There was no significant main effect of hemisphere (F(1,38)=1.046, p=.313 η2=0.027). A significant interaction was apparent between hemisphere and group (F(1,38)=5.211, p=0.028, η2=0.121). There was no main effect of motion type (F(1,38)=1.320, p=0.258, η2=0.034) but there was a significant interaction between the motion type and group (F(1,38)=9.669, p=0.004, η2=0.203). There was no significant interaction between the hemisphere and motion type in all participants, (F(1,38)=0.325, p=0.572, η2=0.008). Equal variances could be assumed throughout.

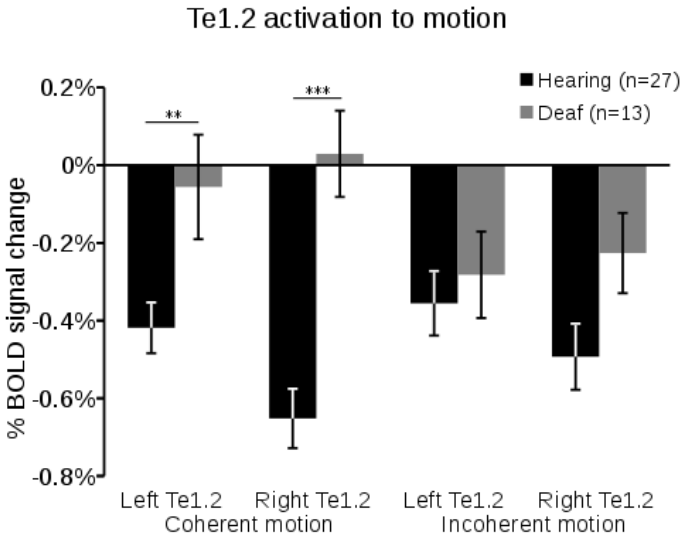

Figure 4.3 – A graph representing mean values of percent signal change in visual motion area Te1.2, divided into hemispheres and motion type, for the deaf and hearing groups. **=p<.01, ***=p<.001. Error bars represent +/-1 SEM.

As there was a significant interaction between the group and motion type, t-test comparisons were conducted to establish where the effect was most prominent. As four comparisons were made the alpha value was Bonferroni corrected to .0125 (.05/4). Firstly, a significant difference was found between groups within the left hemisphere to coherent motion (t(38)=2.745, p=.009). Equality of variances was assumed (F=2.335, p=.135). Within the right hemisphere, the same pattern was apparent for coherent motion, with a significant difference in activation between deaf and hearing subjects (t(38)=5.066, p<.001). Equality of variances was assumed (F=.019, p=.890). There was no difference between groups

in activation to incoherent motion in the left hemisphere (t(38)=.515, p=.610, equality of variances assumed, F=.026, p=.872) or right hemisphere (t(38)=1.873, p=.069, equality of variances assumed, F=.030, p=.864). When presented with coherent motion, area Te1.2 in the deaf participants showed a significantly less suppression bilaterally compared to hearing participants. Conversely, this area was suppressed in hearing participants. This difference between groups is only apparent in the coherent motion condition; activation to incoherent motion shows comparable suppression in both hearing and deaf subjects. Activation is not significantly specific to each hemisphere, but is to the motion type.

4.7.2 Planum Temporale

To investigate possible activation differences in the posterior auditory region, Planum Temporale (PT), a factorial mixed ANOVA was conducted, with factors of hemisphere (left, right) and motion type (coherent/incoherent), and a between subjects factor of group (deaf, hearing). Age was used as a covariate in the initial ANOVA to rule out effects of age upon the results of all participants. Age did not show any significant interactions with either hemisphere (F(1,37)=.042, p=.840, η2=.001) or motion type (F(1,37)=.895, p=.350, η2=.024).

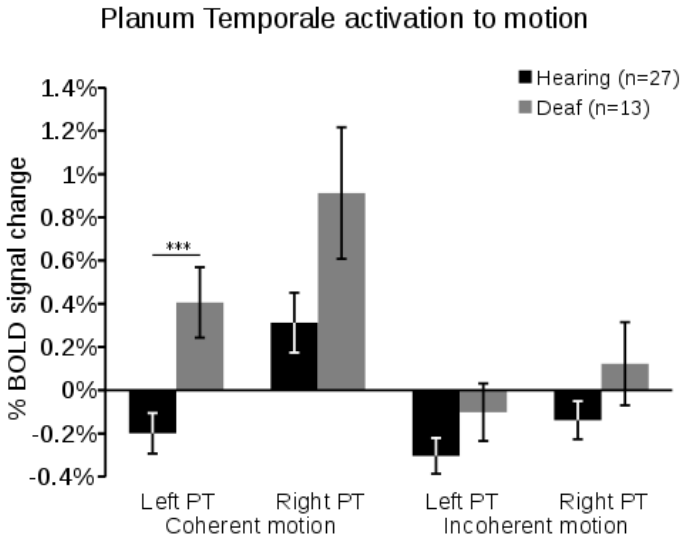

Figure 4.4 – A graph representing mean values of percent signal change in visual motion area PT, divided into hemispheres and motion type, for the deaf and hearing groups. ***=p<.001. Error bars represent +/-1 SEM.

A second ANOVA was therefore conducted, without including age as a covariate (See Figure 4). Test of between subjects effects showed a significant overall difference between

our groups, (F(1)=7.434, p=.010, η2=.164). There was a significant main effect of hemisphere (F(1,38)=9.796, p=0.003 η2=0.205) but no interaction between hemisphere and group (F(1,38)=0.14, p=0.905, η2=0). There was a significant main effect of motion type, (F(1,38)=35.946, p<0.001, η2=0.486). A significant interaction was also apparent between the motion type and group (F(1,38)=5.763, p=0.021, η2=0.132), as well as between hemisphere and motion type in all participants (F(1,38)=34.006, p<.001, η2=0.472). Equal variances could be assumed throughout.

To ascertain where the effect was most prominent, t-tests were conducted within each hemisphere and motion type. The alpha value was Bonferroni corrected to .0125 (.05/4). Within the left hemisphere, a significant difference between the groups was found within the coherent motion condition (t(38)=3.439, p=.001, equal variances were assumed, F=1.578, p=.217). There was no significant difference in the incoherent motion condition (t(38)=1.342, p=.188, equality of variances assumed, F=.216, p=.645). Within the right hemisphere PT activation, there was no significant difference between the groups in the coherent motion condition (t(38)=2.075, p=.045), or in the incoherent motion condition t(38)=1.421, p=.163). Equal variances were assumed in both tests (coherent: F=2.928, p=.095; incoherent: F=3.039, p=.089). The Planum Temporale shows more lateralisation when processing coherent motion. There is a significant difference between deaf and hearing subjects in activation within the left PT, but not in the right PT. Incoherent motion blocks show no processing differences between the deaf and hearing groups.

4.7.3 Heschl's Gyrus

To investigate possible activation differences in Heschl's Gyrus (HG), a factorial mixed ANOVA was conducted, with factors of hemisphere (left, right) and motion type (coherent, incoherent), as well as a between subjects factor of group (deaf, hearing). Age was used as a covariate in the initial ANOVA to rule out effects of age upon the results of all participants. Age did not show any significant interactions with either hemisphere (F(1,37)=.337, p=.565, η2=.009) or motion type (F(1,37)=.000, p=.989, η2=.000).

A second ANOVA was therefore conducted, without including age as a covariate (See Figure 4.5). Tests of between subjects effects showed no overall difference between hearing and deaf participants (F(1)=3.204, p=.081, η2=.078). There was a significant main effect

of hemisphere (F(1,38)=18.685, p<.001 η2=0.330), and a significant interaction between motion type and group (F(1,38)=10.629, p=0.002, η2=0.219). There was no significant interaction between hemisphere and group (F(1,38)=1.844, p=0.182, η2=0.046), and no main effect of motion type (F(1,38)=.316, p=0.578, η2=0.008). There was no significant interaction between hemisphere and motion type, (F(1,38)=1.112, p=0.298, η2=0.028) . Equal variances could be assumed throughout.

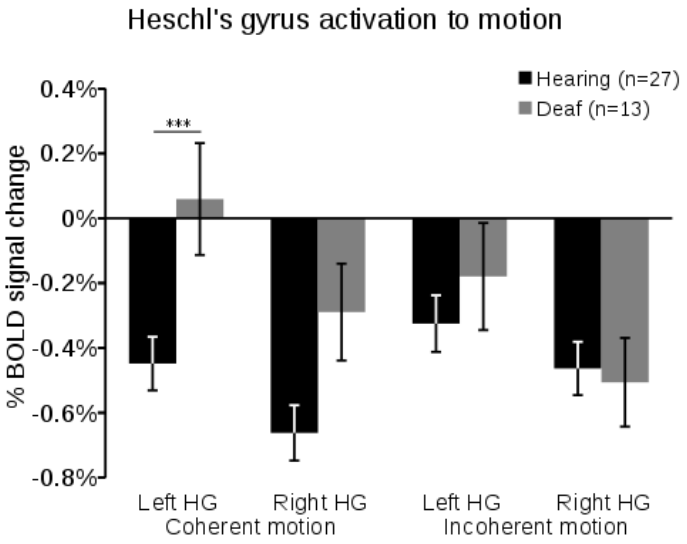

Figure 4.5 – A graph representing mean values of percent signal change in visual motion area HG, divided into hemispheres and motion type, for the deaf and hearing groups. ***=p<.001. Error bars represent +/-1 SEM.

As it was hypothesised that activation profiles would differ between deaf and hearing groups, t-tests were conducted to investigate which comparisons showed this difference. There was also a main effect of hemisphere, as well as an interaction between motion type and group. The significance value was Bonferroni corrected to a value of .0125 (05/4 = .0125). Within the left hemisphere, a significant difference was clear within the coherent motion condition (t(38)=3.017, p=.005, equal variances were assumed, F=3.377, p=.074). There was no significant difference between the groups when considering incoherent motion (t(38)=.857, p=.397, equality of variances assumed, F=.403, p=.529). Within the right hemisphere, no significant difference was observed in either motion type (coherent motion, t(38)=2.321, p=.026, equality of variances assumed, F=.802, p=.376; incoherent motion, t(38)= -.281, p=.780, equality of variances assumed, F=.121, p=.730). Heschl's gyrus, like the Planum Temporale, shows lateralisation, where the left HG is not suppressed by the deaf subjects in the coherent motion condition, whilst the right HG is suppressed in both groups.

4.8 Discussion

4.8.1 Summary of Key Results

The experiment presented in this chapter aimed to identify effects of cortical plasticity in visual motion and auditory regions of the brain, where these differences may result from congenital hearing loss. Behavioural studies have shown visual motion perception advantages in the far-periphery in deaf adults (Buckley et al., 2010; Codina et al., 2017). Therefore, this study sought to identify possible neural substrates involved in far-peripheral motion processing. There were no significant differences between the deaf and hearing participants in the cortical activation to motion within visual areas V5/MT+ and V6. However, the three auditory regions located in the superior temporal cortex showed significant differences in response to motion stimuli between deaf and hearing participants. In the superior temporal cortex, the results indicate that when stimulating the brain with coherent motion, the left hemisphere of deaf participants exhibits significantly different activation in area Te1.2, Heschl's gyrus and the Planum Temporale, compared to hearing individuals. Within the right hemisphere, there is only a significant difference in activation of area Te1.2, where hearing participants showed a strong suppressive signal, whilst the deaf showed one close to null. In the right PT, however, there was an increased response in both groups which was especially pronounced in the deaf participants. Incoherent motion did not yield any activation differences between groups, in any of the auditory regions of either hemisphere.

4.8.2 V5/MT+

There were no significant differences between deaf and hearing participants in the responsiveness of V5/MT+, however the deaf showed consistently, yet not significantly, lower activation from hearing participants in both hemispheres and to both motion types. V5/MT+ was significantly modulated by motion type, where activation was significantly higher in all participants when coherent motion was perceived, compared to incoherent motion. There is some evidence in the fMRI literature showing heightened activation or wider spatial extent of activity in V5/MT+ (Scott et al., 2014; Bavelier et al., 2001), whilst other studies, along with the results of this experiment, show no difference in responsive-

ness in this region between deaf and hearing subjects (Finney and Dobkins, 2001; Bavelier et al., 2000). It is important to consider the discrepancy between these results. Differences reported by Bavelier et al. (2001) were attributed to differences in attentional shifts, as participants were instructed to direct their attention either to central, or peripheral locations. The effects were larger for attention towards peripheral vs. central motion stimuli in deaf participants, with the opposite effect in hearing controls. Similarly, Scott et al. (2014) contrasted responses of attending towards peripheral over central visual targets. It is possible that no effect was present in the current study, as attention was not directed to different visual field eccentricities. However, findings of attentional advantages in deaf individuals have not been replicated in other studies on attentional effects. Bosworth and Dobkins (2002) did not report any differences in attentional capacity between deaf and hearing individuals, when using a direction of motion discrimination task. Similarly, an fMRI study by Fine et al. (2005) did not report any differences in attentional modulation of visual areas, including area V5/MT+, in deaf participants. It is possible that the inconsistency in attentional effects observed across these studies are related to task differences. Differences in activation seen in Bavelier et al. (2001) may be related to the behavioural advantages seen in deaf individuals in peripheral motion processing; however results to this date are inconclusive. A very recent behavioural study by Samar and Berger (2017), offers a further explanation to this inconsistency. They argue that in terms of attentional capacity, reductions seen in central processing of deaf individuals are not necessarily met with enhancements in peripheral processing. It is likely that the spatial distribution of visual performance enhanced by attentional processes in deaf individuals are driven by cross-modal plasticity mechanisms, which recruit specific sensory and multisensory cortices to achieve specific processing enhancements. In contrast to previous studies, the current study investigated the magnitude of percent BOLD signal change, and not the spatial extent of activation (mm^3) as shown in Bavelier et al. (2001). In order to compare results, the number of voxels over a significant threshold ($z>2.3$) were also extracted in the current study, but did not show any significant differences between the deaf and hearing individuals (appendix A.2). It is also worth noting that the extent of visual field stimulated in the Bavelier et al. (2001) study was limited compared to the wide-field motion stimulus used in this study. Here, the motion stimulus used incorporated integration reaching 72° of eccentricity along the horizontal plane.

4.8.3 TO-1 and TO-2

It is also possible that this study did not detect effects within V5/MT+, as the signals were averaged across the entire region, which incorporates several sub-regions. Primate literature provides evidence of at least four separate regions within the MT+ complex, namely MT, MST, FST and tV4 (Ungerleider and Desimone, 1986). These have been shown to have different functional characteristics (Saito et al., 1986). TO-1 and TO-2 are well established human homologues of areas MT and MST (Huk et al., 2002; Amano et al., 2009; Cardin et al., 2012b). TO-1 has been shown to respond strongly to all types of motion, whilst TO-2 is modulated by complex motion such as expansion and rotation, responding less to translational and random motion (Smith et al., 2006). Populations of neurons in area TO-2 have larger receptive fields, but the area does not have a distinguishable retinotopic map. TO-2 could be responsible for integrating motion over a larger visual field extent. TO-1 has smaller receptive fields, and a representation of the contralateral hemifield (Heeger et al., 1999). Some previous research has suggested that receptive fields coding the periphery are larger in the primary visual cortex (V1) of deaf individuals, compared to hearing controls (Smittenaar et al., 2016). It is not known whether this difference is present, or modulates differential responses, in area V5/MT+. By averaging signals across the sub-regions TO-1 and TO-2, this study may have lost some sensitivity in its ability to detect differential activation between hearing and deaf participants. Further research could investigate weather activation profiles between deaf and hearing individuals differ within the sub-region of the V5/MT+ complex especially within area MST which integrates over a larger portion of the visual field. Also, it is possible that previous studies (Bavelier et al., 2001; Fine et al., 2005) report group differences mainly from area TO-1, as the limited visual field stimulated would not incorporate the receptive fields which respond far into the periphery as those of region TO-2.

4.8.4 Defining V5/MT+

Localising regions of interests for analysis in fMRI always poses challenges. In the present study, the region was defined by choosing a restricted sum of three different definitions of V5/MT+. This conservative approach allowed signals from V5/MT+ to be extracted with a high degree of reliability. A future study could introduce careful retinotopic map-

ping procedures (Amano et al., 2009) or functional localisers for areas TO-1 and TO-2 (Huk et al., 2002), which would provide a way of defining the two regions separately, and extracting comparable activation within them. This could elicit possible differences in activation as well as receptive fields between the activation of TO-1 and TO-2 between deaf and hearing individuals, identifying one of the sub-regions as a substrate of heightened far-peripheral motion processing.

4.9 V6

Activation in area V6 did not differ between deaf and hearing individuals. All participants did show higher activation in contralateral V6 to coherent motion, as seen in previous studies (Pitzalis et al., 2006; Fattori et al., 2009a). This is observed especially when the perceived motion is egomotion compatible, such as coherent motion of optic flow fields (Cardin and Smith, 2011; Cardin et al., 2012b). It is possible that, even though V6 has a large peripheral emphasis, it is not directly involved in the heightened behavioural visual advantages seen in the far-periphery of deaf individuals (Buckley et al., 2010; Codina et al., 2017). This question will be further explored in Chapter 6. In animal studies, area V6 shows reciprocal connections with various visual and parietal regions, and plays an essential role in the dorsal visual stream (Galletti et al., 2001). This paper suggested that V6 may be responsible for extracting local information from near reachable space from egocentric global motion, to guide and coordinate arm movements. In this sense, the role of V6 may be to distribute visual information from the dorsal visual stream to parietal regions involved in these sensorimotor actions. V6 has a large peripheral visual field representation, and further studies involving the extrapolation of local motion from global ego-compatible motion fields could elucidate any differences in these tasks, in connection to the behavioural advantages seen in the deaf population.

4.9.1 Localisation of V6

Cardin and Smith (2011) presented reliable ways of localising V6 with ego-compatible motion fields, and Pitzalis et al. (2006) show that the region can reliably be localised through wide-field retinotopic mapping methods. It is quite a focal region, tucked into

the top of the parietal occipital sulcus. In this study, a method of contrasting coherent over incoherent motion blocks was used to identify the region of interest, which reliably captures the core activation of V6. The definition was based on the group average coordinates of the activation clusters which emerged from the mentioned motion contrast (coherent>incoherent). As the definitions used to investigate V6 were focal and limited to a sphere of 20mm in diameter, it is possible that due to individual variability, in some cases these defined mask did not encapsulate V6 activation ideally. A future study could include a functional localiser of V6 motion, in order to identify V6 in each individual, and then query the identified region with a separate motion scan.

4.10 Auditory Cortex

The current study found selective cross-modal activation of auditory cortex in deaf individuals, in line with previous studies (Fine et al., 2005; Finney et al., 2003). Furthermore, coherent motion elicited notable differences in the recruitment of auditory regions between deaf and hearing participants. Significant differences were seen in the responses of bilateral Te1.2 and Heschl's Gyrus, as well as in the left Planum Temporale. Hearing individuals suppressed regions Te1.2 and HG in both hemispheres significantly more than deaf participants. There were no group differences in responsiveness of the auditory regions to incoherent motion (see Figure 4.6). Before discussing the results of the auditory regions, it is important to note that regions of auditory cortex in humans are not as well defined in terms of precise anatomical location or functionality, as they are in animal models (Hackett, 2011; Dick et al., 2012). Furthermore, auditory areas are not as well understood as visual regions of the human brain (Wandell et al., 2007).

4.10.1 Right Auditory Cortex

Hemispheric differences between deaf and hearing participants are highlighted by selective responses to coherent optic flow motion. The right PT is recruited by both hearing and deaf individuals, however this effect is significantly higher in deaf, when compared to hearing participants. In hearing individuals, the right PT is involved in processing auditory motion (Griffiths et al., 1998; Baumgart et al., 1999). A more recent study by Bola et al. (2016)

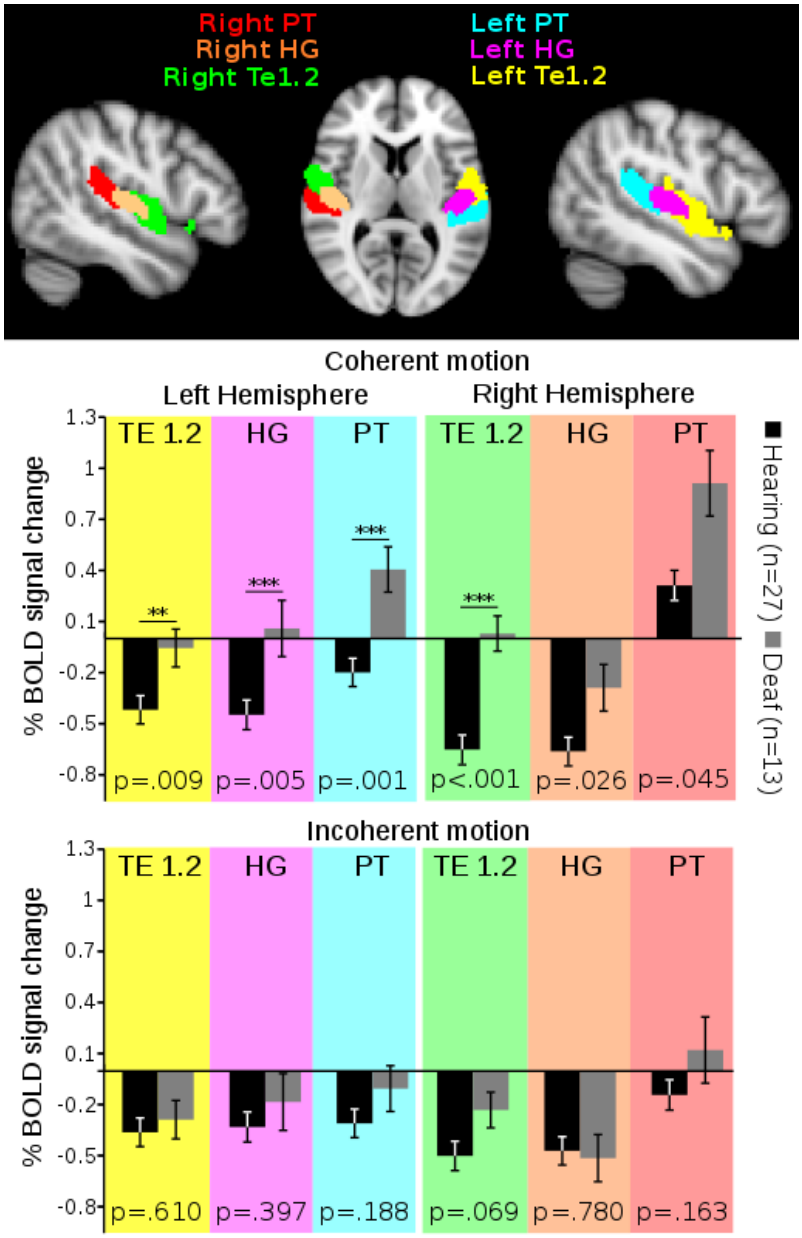

Figure 4.6 – The upper part of the figure shows each auditory region of interest queried in analysis, displayed on the standard MNI152 brain. The bar graphs present the average % BOLD signal change in each group, separated by motion type and auditory region of each hemisphere. Significance indicated after Bonferroni correction. *** = .001, **=.01. Error bars represent +/-1 SEM.

conducted an experiment involving temporal judgements of visual and auditory rhythm in deaf and hearing subjects. Hearing participants were given auditory stimuli, and deaf participants were presented with a visual rhythm stimulus. The higher-level right auditory cortex (posterior-lateral region) showed higher activation during these tasks for both deaf and hearing subjects. This cross-modal activation did not extend to primary auditory cortex in their study. Their results suggest that higher level auditory regions switch their input modality from auditory to visual signals, preserving task-specific activation patterns in this region that are independent of the sensory modality. In the light of current results, the right PT may be recruited to a greater extent in deaf individuals than in hearing individuals. This is likely to be due to the auditory spatial information being absent in the case of deaf individuals. The results of this study support the hypothesis that the right hemisphere PT is most likely involved in the processing and integrating of spatial information, independent of modality. In deaf individuals, this region is recruited to process visual information, given the absence of auditory inputs. This study found a suppressive response in the PT for hearing participants. This can be explained given the possible role of the PT in the integration of sensory inputs. When only one input modality is presented (in this study, coherent optic flow visual motion), suppression is observed in hearing adults as only visual inputs are relevant. Deaf individuals however need not suppress this region, as there is no perceived lack of auditory input. Finally, this study provides novel results where a differential pattern of activation is observed in auditory cortex of deaf and hearing individuals only when coherent, and not incoherent, wide-field motion is considered (see Figure 4.6).

4.10.2 Left Auditory Cortex

Activation increases in deaf compared to hearing participants within the left auditory cortex, when progressing from area Te1.2, through HG and PT. Again, the PT is activated more so in deaf individuals when compared to the hearing group (see Figure 4.6). In terms of functionality, the left auditory cortex of hearing individuals is optimised for processing speech as it has a higher sensitivity to spectral information (Zatorre et al., 2002). The left HG shows enhanced responses when hearing individuals integrate auditory and visual speech signals (Calvert et al., 2001). In deaf individuals, the left PT shows recruitment during a mouth-movement matching task (Sadato et al., 2005). An fMRI study of deaf

and hearing subjects, both separated into groups of signers and non-signers (Cardin et al., 2013), observed activation in the left superior temporal cortex. This activation was tied to language processing, regardless of its input modality, and right superior temporal cortical activation was specific to auditory deprivation. This study did not include language based stimuli in either modality. However, based on the outlined studies, the left auditory area might still be language specific and not tied to a specific modality. This may be the case especially in more central and anterior parts (Te1.2 and HG), as the PT appears to be specifically involved in processing visual motion, as this study found selective recruitment for processing coherent motion in the left PT of deaf, but not hearing individuals.

4.10.3 Bilateral Auditory Cortex

The anterior auditory area Te1.2 is not activated by coherent motion in deaf individuals, but is significantly suppressed bilaterally in hearing when compared to deaf individuals. Incoherent motion showed no differences between the groups. Previous studies, such as that of Karns et al. (2012), found the largest responses to somatosensory stimuli within the more anterior area Te1.2 in deaf individuals. This correlated with the perceived strength of a double-flash illusion, signifying the regions plasticity and involvement in multisensory processing. Overall, the current study found significant evidence showing that auditory cortex is distinctively modulated by coherent wide-field optic flow fields. This is an interesting finding as previous studies found that hearing signers did not show any activation of auditory cortex to visual stimuli (Fine et al., 2005). One explanation for this is that studies often look at activation contrasts between groups (Fine et al., 2005; Karns et al., 2012; Scott et al., 2014), in which case the contrast of deaf over hearing responses could either mean that hearing suppress the region more or deaf participants activate it more, or not at all. The current study includes the percent BOLD signal change and not contrasts, therefore providing a more accurate picture of neural responses. In line with this point, it is also important to note that the suppression of auditory regions Te1.2 and HG observed in the hearing group across both hemispheres is not due to the suppression of scanner noise as when viewing incoherent motion, the deaf and hearing participants follow the same activation pattern in all auditory regions.

4.10.4 Localisation of Auditory Regions

It is important to note that the location of auditory cortex is highly variable across individuals, and is more susceptible to error when localising it through a brain atlas (Karns et al., 2012). This is compounded by the fact that there are a number of functional and anatomical subdivisions within auditory cortex, whose precise definition in humans is still unclear. Methods such as those used by Dick et al. (2012) use structural properties of the auditory cortex based on myelination to accurately identify the core of primary auditory cortex. Their study nonetheless noted inter-hemispheric variability within individuals, as well as noticeable differences between subjects. Despite the fact that, in this study, regions of interest were defined using brain atlas masks, there was a striking difference between coherent and incoherent motion in the selected regions of the primary and higher-level auditory regions.

4.11 Visuo-spatial Language Experience

These data likely represent the effects of sensory deprivation rather than language modality differences. Previous studies that included hearing signers as an additional control group did not show significantly increased activation over that observed in deaf participants in primary auditory, V5/MT+ and STC regions (Neville and Lawson, 1987; Bavelier et al., 2001). Although British Sign Language interpreters have shown motion detection advantages over hearing non-signers, the deaf still displayed the greatest behavioural advantage out of the three groups (Codina et al., 2017).

4.12 Conclusions

In conclusion, the presented results have highlighted that regions of heightened visual motion processing seen in deaf individuals might not be located in sensory specific visual regions, but within cross-modal regions in the superior temporal cortex. When comparing deaf to hearing controls, there was no recruitment in regions Te1.2 and HG in either hemisphere. This study did, however, observe higher recruitment of the Planum Temporale, especially in the right hemisphere. These results show novel and distinctive differences in

response profiles in auditory regions between deaf and hearing participants, when visual information in the shape of coherent global motion is processed.

Chapter 5

Behavioural Measures of Motion Processing in Deaf and Hearing Adults

5.1 Overview

This chapter describes two behavioural tasks designed to measure differences in peripheral visual motion processing in deaf individuals, when compared to hearing controls. The background literature is described, where previous evidence of visual processing differences between deaf and hearing individuals is outlined. The first task carried out by participants measured visual global motion discrimination, where participants had to judge the direction of coherently moving dots, amongst incoherent dot motion. This task was designed to maximally stimulate motion regions V5/MT+ and V6, described in Chapter 4, to relate behavioural outcomes to neural responses in these regions. The second behavioural experiment targeted local motion detection, where participants were asked to detect slow motion changes at various eccentricities. This paradigm was closely matched to tasks used previously in the literature, in which deaf individuals showed superior performance. The testing methods are described in brief, followed by the results of both tasks. Measures of performance thresholds and reaction times were extracted and compared. The results of the two tasks are discussed in light of each other and previous literature.

5.2 Background

In congenital deafness, the lack of auditory signals are often paired with superior visual performance when compared to normally hearing adults. These differences in visual perception are likely due to sensory compensation. The performance of deaf individuals compared to hearing controls has been studied with various visual tasks (Neville and Lawson, 1987; Loke and Song, 1991; Bavelier et al., 2000; Proksch and Bavelier, 2002; Stevens and Neville, 2006; Hauthal et al., 2013; Heimler and Pavani, 2014, Shiell et al., 2014, Codina et al., 2016). However, the current literature does not present a clear case for advantages in every type of visual task, and it appears that it is not simply a matter of superior or inferior visual processing abilities of deaf individuals. Rather, deaf participants may show selective enhancements within specific types of visual processing. A review by Pavani and Bottari (2012) summarised several behavioural experiments which investigated the performance of deaf and hearing individuals in various sensory tasks. They concluded that a number of experiments demonstrate superior behavioural advantages in the deaf population when a task included manipulations of visual attention (Bavelier et al., 2000; Neville and Lawson, 1987; for a review, see Voss et al., 2010). Building on this notion, several publications have showed enhancements in attentional processing involving spatial localisation of visual targets in the peripheral visual field (Parasnis and Samar, 1985; Loke and Song, 1991; Bosworth and Dobkins, 2002; Proksch and Bavelier; Bottari et al., 2010). Furthermore, deaf adults appear to show enhancements in the peripheral visual field in motion processing (Bavelier et al., 2000; Stevens and Neville, 2006; Buckley et al., 2010; Hauthal etl al., 2013).

One example where motion processing is particularly heightened in deaf subjects includes discrimination of motion, where Hauthal et al. (2013) employed a task with coherently moving and static dots. These were presented in two apertures on either side of a centred fixation point at 6.25 ° eccentricity. Deaf and hearing individuals did not differ in their ability to localise movement. However, when asked to discriminate small angular differences in the direction of dot motion, the deaf participants responded faster and more accurately. When considering these findings, the study by Hauthal et al. (2013) only stimulated the near peripheral visual field (6.25 °). There is a high variability in the many tasks used to investigate visual processing enhancements, as definitions of central vs. pe-

ripheral visual field vary drastically. Studies describing 'central' visual field can vary from direct, central fixation to perifoveal locations, whilst 'peripheral' conditions have been used to describe anything from 3-25 ° eccentricity. Anatomically within the retina, the foveal region is clearly defined and extends to 1.5 °, whilst the definition of the perifovea varies across studies, and can describe eccentricities between 1.5-10 ° (discussed in Burnat, 2015). It is important to make these distinctions, as the largest behavioural advantages seem to transpire further within the peripheral visual field. One of the earlier studies by Loke and Song (1991) investigated differences between hearing and deaf subjects in visual target detection tasks. Participants had to detect a visual target on a screen, an asterisk which appeared centrally at fixation (0.5 °) or peripherally (25 °). The deaf group was significantly faster in the peripheral condition, but also showed faster, yet not significantly so, reaction times in the central condition. At further eccentricities, a kinetic perimetry test, where a subject has to detect a dot moving in from the far periphery and a dimmer light into the near periphery, demonstrated higher sensitivity in deaf individuals within both the near (30 °) and far periphery (< 60 °) (Buckley et al., 2010). It is perhaps not by chance that the observed enhanced sensitivity emerges within further eccentricities. Auditory and visual inputs coming from the periphery are used to monitor the surrounding environment for changes and hazards. Auditory signals are especially useful in providing information originating beyond the visual field, and hearing individuals benefit from auditory signals orienting them towards potential risks. It is therefore possible that with the absence of the auditory input in deaf individuals, peripheral vision compensates for the lack of cross-modal integration of these inputs.

Furthermore, behavioural studies of hearing and deaf subjects do not report advantages in deaf individuals in all types of visual tasks (Bavelier et al., 2000; Stevens and Neville, 2006; Hauthal et al., 2013). The selectivity of perceptual enhancements in deaf individuals was investigated by Lomber et al. (2010) using a wide range of visual tasks, including visual target localisation, grating acuity, vernier acuity, velocity discrimination and the detection of motion. The study shows a clear specificity of perceptual enhancements. Perceptual advantages of deaf cats were only seen for visual target localisation within the far-periphery, and motion detection tasks. Furthermore, a visual task which modulated attention showed a perceptual deficit in deaf individuals, where heightened sensitivity within the periphery occurred at a cost of lower visual performance in the central visual field (Proksch and Bavelier, 2001). However, there are studies that do not support this hypothesis - no visual

processing advantages were detected in several visual processing studies involving deaf subjects (Reynolds, 1993; Finney and Dobkins, 2001). Interestingly, there have been no detected advantages in studies including deaf children either (Zarfaty et al., 2004). However, a study by Codina et al. (2010) detected visual processing enhancements emerging in adolescents (age 13-15), but not in children, below the age of 12. There is evidence to suggest that differences between the performance seen in the central and peripheral visual field locations of deaf and hearing individuals may not in fact transpire only from differences in the allocation of attention. A study by Bottari et al. (2010) aimed to address this question with two tasks, one requiring the orienting of attention, and the other relying on distributed attention, both tasks involving the same central and peripheral targets. The study showed that the peripheral visual advantage of deaf individuals remained, as they performed better than hearing controls within the peripheral condition, regardless of the attentional manipulation. The result gives support to the argument that it is not down to the allocation of attention per se, but perhaps increased sensitivity in the peripheral visual field which gives rise to the advantage seen in deaf individuals. This heightened sensitivity is not due to faster attentional orienting alone. The described studies which employ near-peripheral motion processing tasks do not consistently report perceptual enhancements in deaf individuals. It is not clear which behavioural advantages are most apparent the variable reports suggest that the advantage is highly selective. The key question is which specific motion processing features deaf individuals are more sensitive to than hearing individuals. However, there is a lack of studies investigating the far-periphery, where motion advantages would be of the highest benefit to deaf individuals, and indeed as mentioned, only a few studies show clear advantages here (Buckley et al., 2010; Stevens and Neville, 2006). The current study addresses this question in the literature by asking whether deaf individuals show faster reactivity or heightened sensitivity to motion stimuli in the far periphery. Here, two distinct motion processing tasks have been designed to investigate both aspects of behavioural performance (perceptual thresholds and reaction times). Both measures are equally informative, and many past studies either only focus on reaction times or only on perceptual thresholds.

5.3 First task: Global motion discrimination

The first behavioural task was carried out to investigate if deaf individuals are better at detecting global coherent motion amongst noise (incoherent motion) than hearing individuals. This was a two-alternative forced choice (2AFC) task, and the stimuli included were designed to target motion processing regions of the brain, in line with the previous chapter, as it was hypothesised that neural motion processing regions V5/MT+ and V6 would be involved in heightened visual sensitivity in deaf adults. Furthermore, as previously discussed, there is reason to believe that the greatest advantage in visual processing in deaf adults is seen when processing far-peripheral motion. Therefore, it was hypothesised that V6, a motion processing area that possesses an enlarged representation of the far-peripheral visual field, might be particularly important for processing far peripheral motion in this task. (The relationship between task performance and visual motion processing in the brain is explored in Chapter 6).

5.4 Second task: Local motion detection

The second behavioural task required participants to detect slow dot motion also in a two-alternative forced-choice (2AFC) task. The paradigm was designed based on experiments which previously show advantages in deaf individuals within the perifoveal visual field, between 5-14 ° (Hauthal et al., 2013, Lomber et al., 2010). In previous studies, deaf individuals showed the enhanced ability to detect motion at lower thresholds compared to hearing controls. The current task extended this paradigm to test far peripheral eccentricities reaching 40 °.

5.5 Methods

5.5.1 Participants

The global motion discrimination task included 33 subjects: 12 congenitally and profoundly deaf individuals (mean age=31.65, range=20- 48 years, 5 females, see Chap-

ter 2, Section 2.1 for more details) and 21 hearing individuals (mean age=25.83 years, range=20-48 years, 11 females). There was no significant age difference between the groups (t(31)=1.955, p=.120). The local motion detection task included 27 subjects: 11 congenitally and profoundly deaf individuals (mean age=29.34 years, range=20-48 years, 5 females, see Chapter 2, Section 2.1 for more details) and 16 hearing individuals (mean age=26.65 years, range=20-48 years, 9 females). There was no significant age difference between the groups (t(25)=0.881, p=.390). All participants had normal or corrected-to-normal vision and gave informed consent. Each deaf participant also filled out a brief questionnaire regarding the known aetiology of deafness (Methods, section 2.2.1). All deaf participants reported severe to profound hearing loss in both ears (>70db). Both studies were approved by The York Neuroimaging Centre Research Governance Committee (Department of Psychology, University of York).

5.5.2 Global motion stimuli

The global motion stimuli were designed to activate the central and far-peripheral visual field and test motion direction discrimination of coherent motion within incoherent motion noise. This type of stimulus was chosen as it strongly activates area V6 (Pitzalis et al., 2006; Cardin et al., 2012) and area V5/MT+ (Smith et al., 2006). These two regions are investigated as correlates of global motion discrimination performance, and possible substrates of higher sensitivity in deaf individuals (see Chapter 6). Stimuli were presented in three conditions testing the central visual field, left far peripheral field and right far peripheral field. In each eccentricity condition, the participant judged the global direction of motion in each run, which was either radial (inwards/outwards) or angular (clockwise/counter-clockwise) (see Figure 5.1). The dependent variable consisted of a threshold obtained, representing the percentage of coherently moving dots needed to identify the direction of motion amongst incoherent dot motion, with a 75% correct response rate. A Bayesian adaptive Weibull staircase was used to fit perceptual threshold values (Kontsevich and Tyler, 1999). In the peripheral conditions, wide-field dot motion was displayed beyond 40 ° from fixation, extending to the edge of the screen, at 89 °, in the left and right hemifield separately. The central condition consisted of an aperture with a 5 ° radius around central fixation, within which dot motion was presented. The size of the dots was scaled according to eccentricity to account for cortical magnification and create

a percept of motion in depth (optic flow) especially within the peripheral conditions (for more details, see Chapter 2, Section 2.10).

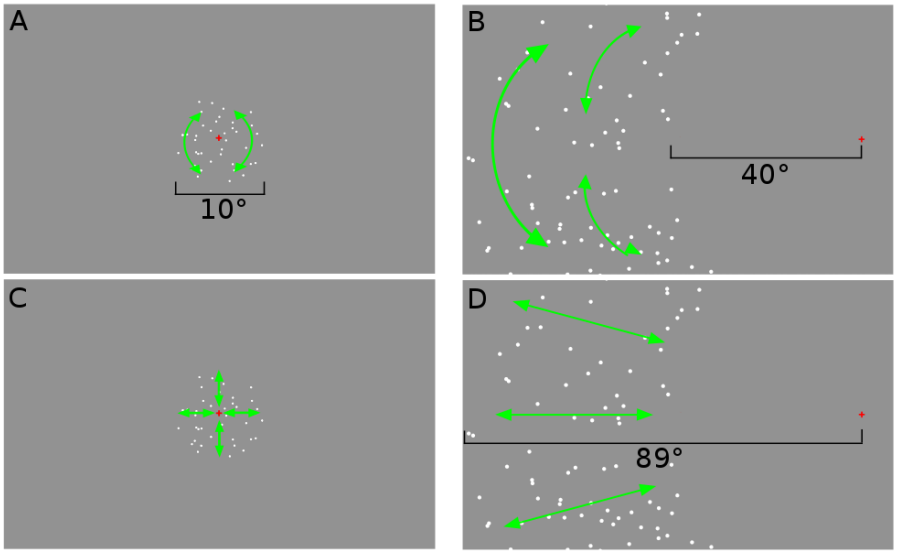

Figure 5.1 – A schematic representation of two eccentricity conditions (central: A, C; left peripheral B,D). The green arrows represent the two possible directions of motion, it being either angular, clockwise/counter-clockwise (A, B) or radial, inwards/outwards (C, D). The right peripheral hemifield condition was a mirror image of the left hemifield condition. The green arrows indicate the two possible angular motion directions (clockwise and counter-clockwise directions).

5.5.3 Local motion stimuli

The local motion task was designed to test the sensitivity of local motion detection at different eccentricities (5 °,10 °,20 °,40 °), including the far-periphery, in contrast to the global motion direction discrimination task. Previous studies with localised motion tasks have reported visual processing advantages in deaf human subjects (Hauthal et al., 2013; Shiell et al., 2014; Scott et al., 2014) and deaf cats (Lomber et al., 2010). The stimuli used in this study consisted of two apertures (9 ° diameter), on either side of the fixation cross. In each trial lasting 500ms, one of the two apertures would contain dots moving (between 0.1 °/sec-1 °/sec) either left or rightwards with 100% dot coherence (for more details, see Figure 5.2 and Chapter 2, Section 2.16). Participants were instructed to indicate which of the apertures contained motion (left or right aperture), but not the direction of dot motion. The dependent variable extracted was the threshold based on the minimum speed necessary for 75% correct motion detection, and a Bayesian adaptive

Weibull staircase was also used to fit perceptual threshold values in this task (Kontsevich and Tyler, 1999). The next trial would start after a response was given.

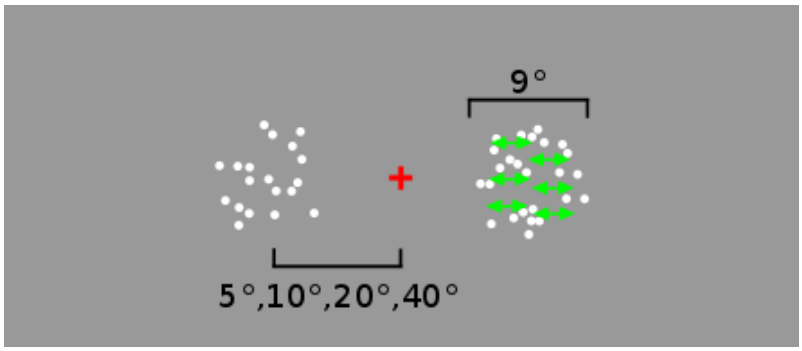

Figure 5.2 – A schematic representation of the four eccentricity conditions included in the local motion detection task. The green arrows indicate the two motion direction possibilities.

5.5.4 Procedure

Both psychophysical tasks used the method of two alternative forced choice (2AFC), and were designed in Psykinematix (Beaudot, 2009). Subjects were seated in front of a large Samsung 51 plasma display in a dark room, at a viewing distance of 600mm. Participants completed at least one practice trial in the 5 ° and 40 ° eccentricity condition, and were asked if they felt comfortable with the task before beginning. Trial order was randomised for both tasks. Every participant carried out each condition at least twice, if the thresholds were in close agreement. If they were not, participants were asked to complete more trials. When testing deaf participants, a BSL interpreter assisted in explaining the task, if needed. Before each run, participants were prompted with written instructions on screen, where they were reminded to keep their gaze on the fixation cross at all times. Responses were recorded through a keyboard. Participants were instructed to respond with their preferred hand. Testing each participant took 40-60 minutes per task, depending on breaks taken between runs and explanation time needed. For further details see Chapter 2, Section 2.17.

5.5.5 Data Analysis

The thresholds from each run were averaged for each condition to provide a mean for all motion sensitivity within a visual location. In the global motion task these included

means for the radial and angular motion runs within the central, left and right peripheral locations, and for the local motion task a mean per each eccentricity condition (5°,10°,20°,40°). Thresholds extracted were averaged for each eccentricity condition. The mean of the median reaction times were recorded for the correct response trials in each condition for both tasks. Responses given before 200ms were discarded, attributed to premature responses or a lapse in attention. For more details see Chapter 2, section 2.18.

5.6 Results

5.6.1 Global Motion Discrimination

As the left and right visual far-peripheral field conditions were separate, possible differences between hemifields were tested with a mixed factorial ANOVA, with the factor of hemifield (left, right) and group (deaf, hearing). There was no main effect of hemifield on threshold ($F(1,29)=.192$, $p=.664$, $\eta 2=.007$) or reaction time ($F(1,29)=.574$, $p=.455$, $\eta 2=.021$). Equal variances were assumed for both measures. There were no significant interactions between hemifield and group (threshold: $F(1,29)=.192$, $p=.664$, $\eta 2=.024$; RT: $F(1,29)=.021$, $p=.866$, $\eta 2=.001$), and there were no overall differences between groups (threshold: $F(1,29)=.604$, $p=.433$, $\eta 2=.020$; RT: $F(1,29)=1.219$, $p=.279$, $\eta 2=.043$). As no differences were shown between hemifield conditions, the thresholds and reaction times for these two conditions were grouped together and averaged to constitute the far peripheral condition. To investigate threshold differences between the deaf and hearing groups, a mixed factorial ANOVA was conducted with factors of eccentricity (central, far peripheral) and group (deaf, hearing). The between subjects test showed no overall difference within the two groups in threshold ($F(1,30)=1.696$, $p=.203$, $\eta 2 =.054$) or eccentricity (central vs. far peripheral), $F(1,31)=2.101$, $p=.157$, $\eta 2 =.063$. There was a significant interaction present between the eccentricity tested and group ($F(1,31)=5.779$, $p=.022$, $\eta 2=.157$). This indicates a group difference, depending on the eccentricity condition in question, where deaf individuals moved towards lower thresholds in the central condition, but the opposite trend is apparent in the peripheral condition, where deaf participants showed higher thresholds (as seen in Figure 5.3.) As the key aim of this experiment was to compare the performance of deaf and hearing groups, and the ANOVA showed an in-

teraction between the eccentricity condition and group, t-tests were conducted to compare means within each condition. In the central and peripheral visual field conditions there were no significant differences seen between the groups (Central: t(31)=-1.635, p=.112; Peripheral: t(31)=-1.253, p=.219; equal variances assumed for both conditions (Central: F(1,31)=1.112, p=.300; Peripheral: F(1,31)=1.693, p=.203). These results are plotted in Figure 5.3.

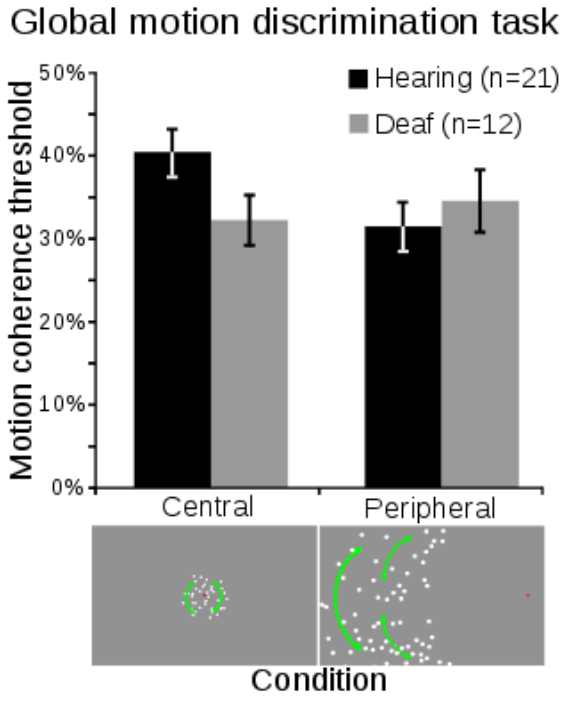

Figure 5.3 – A bar graph which represents global motion discrimination task thresholds, angular and radial motion conditions averaged, which represent the percentage of coherently moving dots necessary for response accuracy of 75%. Plotted means of deaf and hearing groups. Error bars represent 1+/- SEM.

Likewise, to investigate reaction time differences between deaf and hearing participants within the central and peripheral conditions, a mixed factorial ANOVA was conducted with factors of eccentricity (central, peripheral) and group (deaf, hearing) (The results are plotted in Figure 5.4). Firstly, the between subjects test showed no overall difference between deaf and hearing participants (F(1,31)=1.517, p=.227, $\eta 2$ =.047). There was no main effect present for the eccentricity tested (F(1,31)=2.774, p=.106, $\eta 2$ =.082), and no interaction between the visual field condition and group (F(1,31)=.220, p=.643, $\eta 2$=.007). As the key aim of this experiment was to compare the performance of deaf and hearing groups, t-tests were conducted to compare the means of the two groups in each condition. There were no significant differences seen between the groups in the central and

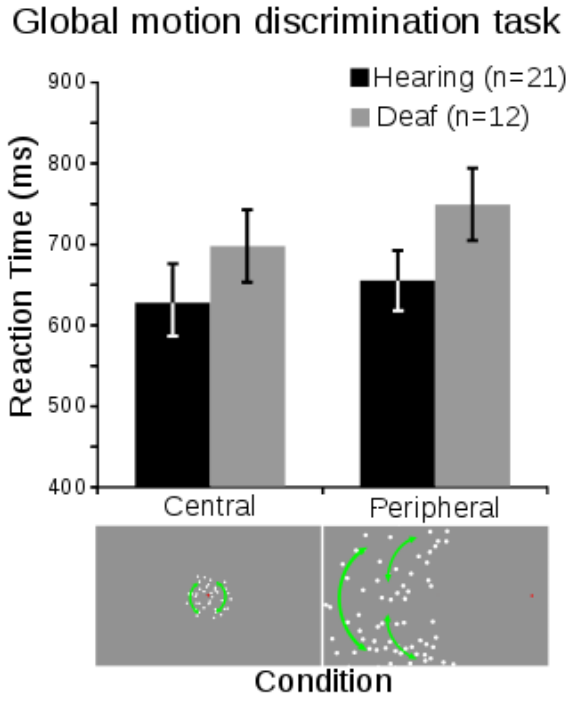

Figure 5.4 – Global motion discrimination task reaction times, angular and radial motion conditions averaged, which represent the reaction times necessary for response accuracy of 75%. Plotted means of deaf and hearing groups. Error bars represent 1+/- SEM.

peripheral visual field conditions (Central: t(31)=.761, p=.452; Peripheral: t(31)=1.454, p=.156; equal variances assumed for both conditions, Central: F(1,31)=.092, p=.764, p=.300; Peripheral: F(1,31)=1.738, p=.197).

5.6.2 Summary of Results: Global Motion

It was hypothesised that deaf participants would perform better, with lower thresholds, in the peripheral motion task; however, the opposite trend was observed. The deaf group had a tendency towards better thresholds in the central visual field, and worse thresholds in the peripheral visual field, which was confirmed by a significant interaction between visual field condition and group. This was however statistically underpowered, and no differences were seen when the group means in each condition were compared. The deaf participants seemed to have slightly slower reaction times compared to hearing participants in both conditions, yet this was not a statistically significant difference.

5.6.3 Local Motion Detection

To investigate threshold differences between the deaf and hearing groups of the local motion detection task, a mixed factorial ANOVA was conducted with factors of visual eccentricity (5°,10°,20°,40°) and group (deaf, hearing)(Shown in Figure 5.5). The between subjects test showed no overall difference between the two groups in thresholds ($F(1,23)=.559$, $p=.462$, $\eta 2 =.024$). As Mauchly's test of sphericity was significant ($W=.114$, $df=5$, $p<.001$), a Greenhouse-Geisser correction was applied. There was a main effect of eccentricity ($F(1.428, 32.833)=53.210$, $p<.001$, $\eta 2 =.698$). There was no interaction between eccentricity and group ($F(1.428, 32.833)=.404$, $p=.602$, $\eta 2 =.017$). As an overall effect was seen between conditions in all participants, pairwise comparisons showed that there was no significant difference between the conditions of 5° and 10°, ($p=1.000$), and the main effect was carried by significant differences between 5° and 20° ($p=.006$), 10° and 20° ($p=.006$), 5° and 40° ($p<.001$) as well as 10° and 40° ($p<.001$). As it was hypothesised that deaf individuals would perform better at this task, t-tests were conducted to compare group means within each eccentricity condition. There were no significant differences between the deaf and hearing groups in any of the eccentricity conditions (5°: $t(13.60)=1.260$, $p=.229$; 10°: $t(24)=1.227$, $p=.232$; 20°: $t(16.69)=1.326$, $p=.203$; 40°: $t(25)=-.285$, $p=.778$). Equal variances assumed for conditions 10° and 40° (10°: $F(1,24)=3.743$, $p=.065$; 40°: $F(1,24)=2.357$, $p=.137$). Equal variances were not assumed for conditions 5° and 20° (5°: $F(1,25)=6.295$, $p=.019$; 20°: $F(1,26)=5.134$, $p=.032$). These results showed that, irrespective of whether participants were hearing or deaf, higher speeds were required to detect motion in the periphery.

Reaction time differences between deaf and hearing participants within the four eccentricity conditions were measured with a mixed factorial ANOVA with factors of visual eccentricity (5°,10°,20°,40°) and group (deaf, hearing)(Shown in Figure 5.6). Firstly, the between subjects test showed no overall difference between deaf and hearing participants ($F(1,23)=.674$, $p=.420$, $\eta 2 =.028$). As Mauchlys test of sphericity was significant ($W=.485$, $df=5$, $p=.008$), a Greenhouse-Geisser correction was applied. Similar to the threshold data, there was a significant main effect of eccentricity condition ($F(2.004, 46.089)=7.144$, $p=.002$, $\eta 2 =.916$), but no interaction between eccentricity and group ($F(2.004, 46.089)=.813$, $p=.450$, $\eta 2 =.181$). As there was a main effect of eccentricity in all participants, pairwise comparisons revealed that reaction times differed significantly

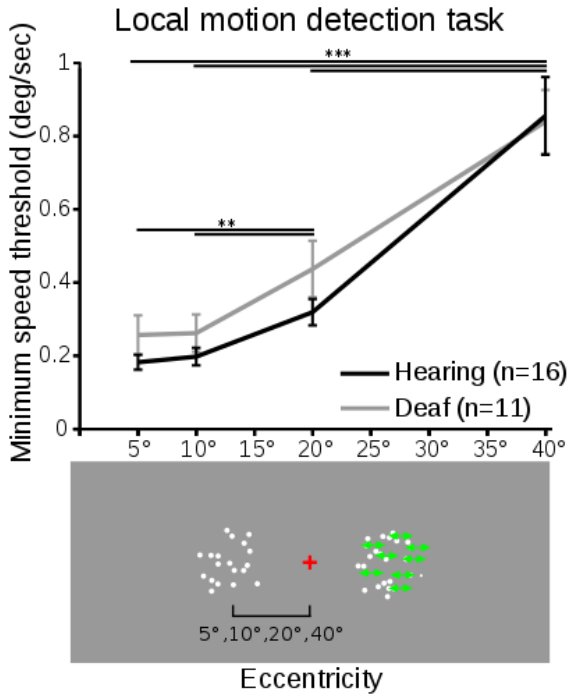

Figure 5.5 – A bar graph which represents global motion discrimination task thresholds, angular and radial motion conditions averaged, which represent the percentage of coherently moving dots necessary for response accuracy of 75%. Plotted means of deaf and hearing groups. Error bars represent 1+/- SEM.

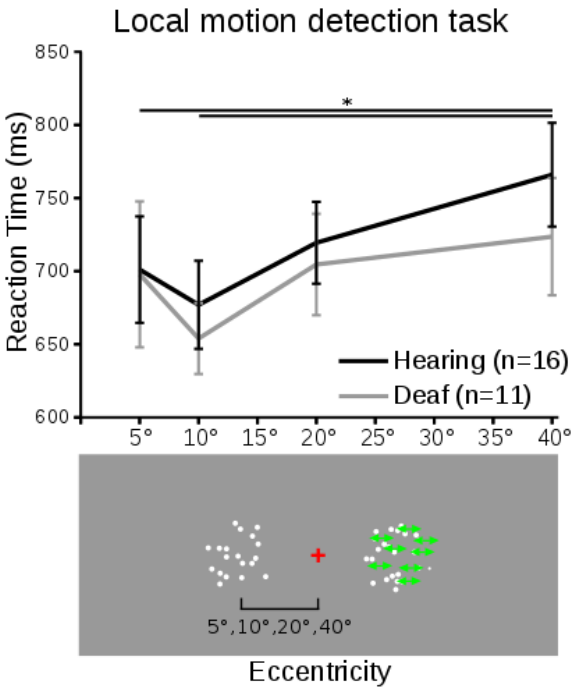

Figure 5.6 – Global motion discrimination task reaction times, angular and radial motion conditions averaged, which represent the reaction times necessary for response accuracy of 75%. Plotted means of deaf and hearing groups. Error bars represent 1+/- SEM.

only between the 5° and 40° conditions (p=.025), whilst the other paired comparisons were not significant (5° and 10°, p=1.00; 5° and 20°, p=.277; 10° and 20°, p=.085; 20° and 40°, p=.400). The mean of the median reaction times of each group were compared within every eccentricity condition, to examine possible group differences. There were no significant differences between the deaf and hearing groups in any of the eccentricity conditions (5°: t(25)=.427, p=.673; 10°: t(24)=-.332, p=.743; 20°: t(26)=-.130, p=.898; 40°: t(25)=-.499, p=.622). Equal variances were assumed for all conditions (5°: F(1,25)=.189, p=.668; 10°: F(1,24)=2.498, p=.127; 20°: F(1,26)=.186, p=.670; 40°: F(1,25)=.127, p=.724).

5.6.4 Summary of Results: Local Motion Task

It was hypothesised that deaf individuals would achieve lower speed thresholds than hearing participants within the more eccentric conditions, 20° and 40°. However, deaf individuals showed a trend towards higher thresholds in the 5°, 10° and 20° eccentricities, with a more substantial overlap with the hearing group in thresholds in the most eccentric condition (40°). The thresholds show a trend towards convergence when moving out to further eccentricities. It was also hypothesised that deaf individuals would show faster overall reaction times, especially when moving into further eccentricities. Reaction times show a trend towards being faster in deaf across all eccentricities, but this trend was not significant.

5.7 Discussion

The present study compared the performance of deaf and hearing individuals in two motion processing tasks, extracting measures of both perceptual thresholds and reaction times. The global motion task required participants to discriminate the coherent motion direction embedded amongst incoherent motion. There was a significant interaction between the thresholds in each condition and group. Deaf individuals, when compared to hearing, showed a trend towards better performance, lower thresholds, in the central visual field condition, compared to the periphery, where their performance showed a trend towards worse performance. This was an unexpected result, as the study hypothesised that deaf in-

dividuals would show a higher sensitivity in the periphery, yet the opposite trend emerged. Reaction times did not differ significantly in either condition; however, also unexpectedly, the deaf individuals tended to show slower reaction times across both conditions. In the local motion task, participants were asked to detect motion of slow speeds in apertures along the horizontal meridian at varying eccentricities. The deaf group showed a trend towards faster reaction times across all conditions, supporting the hypothesis that the deaf group would react more quickly. The mean threshold of the deaf group did not differ significantly compared to hearing individuals, contrary to a study by Shiell et al. (2014) where deaf and hearing individuals detected motion in moving gratings on the horizontal meridian, 10 ° from fixation in each hemifield, where lower motion detection thresholds were observed in hearing participants.

Interestingly, the global motion paradigm does not resemble previous tasks used to study visual processing advantages seen in deaf individuals. It further highlights the specificity of visual advantages in deaf individuals being tied to local and small changes in motion rather than a possible increase in the global percept across a wide field of the far-peripheral motion. For example, Hauthal et al. (2013) showed that deaf individuals are more sensitive to discriminating small changes in the angle of motion direction, and Codina et al. (2010) showed a wider field of sensitivity of the periphery with Goldmann perimetry testing, where participants detect a small visual target which moves from the far-periphery inwards to central fixation. These studies are similar as they both require the detection of small and focal changes, in contrast to the global motion task where participants need to extract the direction of global coherent motion from incoherent motion signals, which need to be ignored. However, in line with the results reported here, Lomber et al. (2010) also did not see any performance enhancements in deaf cats in a motion direction discrimination task. Taken together, it appears that deaf participants show a trend towards a disadvantage in far-peripheral wide-field global integration of motion. Central global thresholds suggested a trend towards better performance in deaf compared to hearing participants, which is in line with previous findings, where motion processing advantages are found in some studies of visual processing in foveal and perifoveal visual fields of deaf individuals. For example, faster reactivity in deaf participants has been reported for the detection of visual targets at eccentricities of 3 ° and 8 ° (Bottari et al., 2010). Considering the current task, detecting a target at slow speeds is likely to require a different approach and may employ different mechanisms compared to the discrimination of coherent global motion direction of dots

within a 10° aperture. Some studies come to the conclusion that auditory deprivation leads to a redistribution of visual attention to the periphery (Dye et al., 2009). Pavani and Bottari (2012) raise the question of which aspect of selective attention this includes: endogenous and/or exogenous attention? The tasks employed in the current study do not introduce any endogenous attentional trade-off effects between visual processing in the central and peripheral visual field. In local motion detection, participants need to divide their attention between the left and right hemifield simultaneously whilst in the global motion discrimination task their attention is spread across a single region containing visual motion (either central or far peripheral). Global motion direction judgements in the far periphery are perhaps more difficult to make as attention needs to be distributed across a large field of moving dots in order to extract a global coherent motion signal within noise, rather than localised uniform coherent motion information, as in the local task. The results of the global motion task suggest that deaf individuals may show more interference from wide-field motion flow fields, leading to lower sensitivity and higher thresholds in the periphery. On the other hand, within the central condition, thresholds trend towards being lower, suggesting higher sensitivity in the deaf participants. This finding relates to those of previous studies, which found visual motion processing advantages for various tasks in foveal and perifoveal locations (Neville and Lawson 1987; Loke and Song 1991; Bottari et al., 2010). The deaf participants showed a possible trend towards faster reaction times in the local motion detection task it is possible that reaction time advantages appear when deaf individuals need to divide their attention across two or more visual locations for detection, as in this case. Bottari et al. (2010) observed notably faster responses in deaf participants in simple visual detection tasks which did not require visuo-spatial competition. The advantages appeared regardless of where the target appeared, not being specific to the periphery (Loke and Song, 1991). In the current task, deaf participants showed a trend towards faster reactions, but they were not met with any indications of higher sensitivity, as thresholds appear slightly higher or the same (at 40°) compared to the hearing group. Both the reaction times and thresholds for the local motion task show a wide spread across participants, making it quite difficult to identify any differences between the groups tested (see appendix A.3).

5.7.1 Comparison of Hemifields

The current study did not detect any hemifield differences in the global motion task. Many studies argue that hearing loss can result in performance lateralisations, where advantages can be specific to either the left or right hemifield. For example, deaf participants performed faster when localising motion in the left, and not right hemifield (Hauthal et al., 2013). In contrast, deaf individuals have also shown faster reactivity in the right visual field, for example when discriminating motion direction in stimuli extending to 15 ° (Finney and Dobkins, 2001), and in other motion processing tasks (Bosworth Dobkins, 1999, 2002; Brozinsky & Bavelier, 2004; Neville Lawson, 1987). Studies aiming to explain these effects have found that enhanced processing in the left hemisphere (and right visual field) are tied to the use of sign-language (Bosworth and Dobkins, 2002b, Cardin et al. 2013). Lateralisation effects also appear to depend on the task at hand, as not all studies find visual processing enhancements to be lateralised. Specific visual tasks may be mediated by sign-language experience. In light of the current findings, this may not be the case when extracting coherent over incoherent motion in a wide field of motion extending to the far-periphery. Lateralisation might therefore only be tied to specific motion tasks, and the results presented here provide evidence of no processing lateralisation in either deaf or hearing individuals within the global motion processing task (see Appendix A.2). Previous studies often focus only on perceptual threshold measures or reaction times. The current study, however, measured both. Preceding studies show faster responses by deaf individuals in both central and near peripheral tasks (Bottari et al., 2011; Bottari et al., 2010). The current study shows a trend towards faster reactivity in the local motion detection task in line with previous studies investigating focal changes in target location and motion (Hauthal et al., 2013; Lomber et al., 2010; Bottari et al., 2010). The global motion task however highlights different aspects of motion processing, where deaf individuals show a trend towards a disadvantage, in the form of slower reaction times in both central and far-peripheral global motion processing. Considering thresholds alongside reaction times is of interest, as better perceptual thresholds do not imply faster reaction times. Indeed, deaf individuals tended to show slower reaction times in all global motion conditions, yet their central visual field thresholds were better, and peripheral threshold worse, when compared to hearing participants. This suggests that there is no speed/accuracy trade off as reaction times show the same result across conditions, but thresholds do not. This also

implies higher sensitivity to motion, but no faster reactivity of deaf individuals. The local motion task performance shows the reverse, where deaf individuals show an overall trend towards faster reaction times, but worse thresholds. These results could suggest that deaf individuals are either less sensitive to local motion detection, or show a trend in faster reactivity, at a cost of worse thresholds, compared to hearing individuals.

5.7.2 Limitations

In both tasks, participants were instructed to keep their gaze on the central fixation cross. In the local motion paradigm, they had to monitor two apertures in the left and right hemifield, and the global task required them to attend to either left, right or central visual field. The study did not employ any objective assessments of eye movements, and cannot completely exclude possible confounds created by gaze shifts during testing. Participants were given clear instructions to keep their gaze on the fixation cross at all times however, and the experimenter was present during practise trials to ensure the participant understood these instructions. Overall, both tasks would benefit from larger sample size to increase statistical power allowing the study to identify significant differences in performance between deaf and hearing participant groups. The local motion paradigm extended past experiments by extending to 40 °, however further investigations could explore effects beyond 40 ° eccentricities as well, to find out if deaf individuals would show better perceptual thresholds. Previous work shows that visual advantages are most prominent at 60 ° and beyond (Codina et al., 2016). A possible manipulation could include one where the stimulus apertures are presented in each hemifield along the horizontal meridian but with a larger field of view, or alternatively, the apertures could be positioned within the same hemifield, above and below the horizontal meridian. The expected results of these experiments would show faster reaction times in further eccentricities of deaf individuals, met with better thresholds, in line with findings of higher sensitivity (Buckley et al., 2010) and faster reactivity (Codina et al., 2016) in the far-periphery. Considering both tasks used in this study, one can ask which situation is more ecologically valid, and would provide a benefit to deaf individuals. It is possible that the division of attention is crucial, where visual targets are competing, and being able to monitor central and peripheral visual fields equally results in a benefit in the form of faster reactivity regardless of the target location in the visual field. In the case of Goldmann perimetry tests (Buckley et al., 2010),

attention is distributed equally across the whole visual field, and participants know that the target will appear in either the near or far periphery, at any cardinal location within the visual field. Whilst the stimuli in the aforementioned behavioural studies used very focal localised motion detection paradigms, the wide-field optic flow motion spreads over a very wide extent of the visual field, where it is not a matter of detection but the extraction of coherent motion from a global percept. It is possible that far-peripheral visual field advantages observed in deaf individuals are specific to local detection, and divided attention, rather than global motion processing, where attention is widespread.

5.7.3 Summary

The results of this study show that deaf individuals move towards trends of slower reaction times in global motion discrimination, but faster reaction times in local motion detection. More localised motion detection tasks seem to be met with enhanced visual perception in deaf participants, in the form of faster reactivity. Enhanced reaction time is seen when detection judgements are performed, however extracting motion from global fields of coherent and incoherent motion seems more taxing for deaf individuals. This would suggest that these advantages can be more specific to more focal and detailed changes at all eccentricities, as seen in local motion and central global motion tasks, rather than peripheral global motion processing. The effects are not likely based on preferential allocation of attention to the periphery. However, in the global motion task, results showed the same reaction time patterns in eccentricity tasks, but a clear dissociation between the central and peripheral thresholds. Therefore, attention needs to be equally spread across all locations of the visual field. Along the results discussed, it would appear that deaf individuals might be better at detecting smaller changes within the periphery, and be better at extracting motion signals from noise in the central visual field.

Chapter 6

Neural correlates of motion perception in deaf and hearing adults

6.1 Overview

This chapter investigates links between brain and behaviour, exploring neural substrates of visual motion processing differences between deaf and hearing individuals. Numerous studies identify either behavioural or neural differences in deaf individuals, when compared to hearing, but only a select few attempt to relate functional and structural measures with behavioural advantages. This chapter begins with a general overview of the literature which describes previous investigations of neural substrates of perceptual advantages apparent in the deaf population. Structural measures and neural responses are then correlated with two psychophysical motion processing tasks, all described in the previous chapters. The first part of this chapter describes correlations between structural V1 measures and motion processing performance in global and local motion tasks. The second part includes functional measures of BOLD activation to optic flow motion in visual and auditory brain regions, and correlates this with visual motion task performance.

6.2 General Background

Investigations of neural substrates of heightened visual sensitivity in deafness using animal models have been highly successful, such as those involving congenitally deaf cats (Lomber et al., 2010). The researchers found that deaf cats were better at certain visual tasks, and found a correlation between auditory regions and visual motion detection and the detection of targets in the periphery. When the dorsal zone (DZ) and posterior anterior field (PAF) of cat auditory cortex were selectively disabled, visual performance advantages in respective tasks were erased and the deaf cats performed just as poorly as their hearing controls. This evidence shows clear causality between sensory deprivation, leading to cross-modal plasticity and the identification of neural substrates underlying heightened visual motion processing sensitivity. Few neuroimaging studies of deaf humans have attempted to relate structural and functional measures to behavioural performance outcomes on visual tasks, and not many provide strong or conclusive results. A large number of human neuroimaging studies demonstrated that the absence of hearing from an early age can cause the brain to reorganise visual processing resources (Neville and Lawson, 1987; Finney et al., 2003; Bavelier et al., 2001; Fine et al., 2005; Hauthal et al., 2013; Scott et al., 2014). However, in these studies no measures of behavioural differences between the two groups were taken. This makes it impossible to state whether these neural differences are directly related to advantages or disadvantages in visual processing. Whilst numerous behavioural studies are able to detect advantages in deaf individuals visual processing abilities (Hauthal et al., 2014; Bottari et al., 2010; Loke and Song 1991), they can only speculate as to the neural substrates which facilitate the observed heightened visual sensitivity. The aim of this chapter is to bridge this gap by relating the observed structural and functional neural differences with behavioural performance, as only a select few studies have attempted this. An example of a study which did so successfully (Bottari et al., 2011) measured event-related brain potentials in deaf individuals when performing a speeded visual detection task. Deaf participants responded faster than hearing individuals, and behavioural advantages were related to early visual cortical responses; N1 peak amplitudes were linearly related with the reactivity in both deaf and hearing individuals, whilst only in deaf individuals did the reaction time decrease linearly relative to the P1 peak amplitude. More recent examples include structural measures of auditory cortex and their correlation with visual motion detection. Shiell and Zatorre (2016), including only deaf participants, found

that measures of fractional anisotropy, radial diffusivity and mean diffusivity within the right Planum Temporale (PT) were correlated with visual motion detection thresholds. Both studies provide compelling evidence of possible neural substrates. A further step to take in inferring which neural regions facilitate behaviour would be to closer match the behavioural tasks with the stimuli used to evoke neural activation. A good example of relating structural measures to behavioural advantages seen in deaf individuals included structural measures of the retina, specifically peripheral neural projections which were correlated with peripheral visual field sensitivity (Codina et al., 2010). Inspired by this, the current study matched the section of visual field stimulated within the neuroimaging procedures and behavioural tasks. This achieves a closer match between the stimulus used to evoke activity in regions of interest in the brain, and the behavioural tasks used to measure perceptual advantages in motion processing. By correlating behavioural and neural measures, this study aimed to establish whether neural measures of structure and neural activation show a relation to behavioural performance in the motion processing tasks described in the previous chapter. As described in Chapter 3, a significant difference between deaf and hearing individuals was observed in the amount of cortical surface area dedicated to far-peripheral and central processing. This structural measure was therefore used to investigate whether this difference between deaf and hearing is related to task performance. Furthermore, although not all measures showed differences between deaf and hearing individuals, seeing the relationship between neural and behavioural measures can elucidate the spread of results on a spectrum, rather than comparing these in a category-constrained manner. The wide-field optic flow motion stimuli presented in the fMRI paradigm were closely matched to the global motion behavioural task designed to target motion processing regions of the brain within V5/MT+ and V6. The local motion detection task was carried out at various eccentricities. As V1 was divided into 3 regions, corresponding to different visual field representations, it was possible to relate visual field stimulated and the corresponding neural representations of visual regions in V1. Both motion tasks were correlated with measures extracted from auditory cortical regions, to investigate the influence of cross-modal plasticity upon motion perception performance.

6.3 Part 1: Structural Measures

Is surface area in V1 related to task performance in the corresponding visual field?

Previous fMRI studies have been able to relate cortical measures of V1 to individual perceptual performance in normal hearing participants. Several studies compared the cortical magnification function in V1, which represents the relative proportion of cortex dedicated to processing a section of the visual field as a function of eccentricity. One such study included the Ebbinghaus illusion of relative size misperception, where the larger the central cortical surface area measures of V1 were, the weaker the strength of perceived illusion was (Schwarzkopf and Rees, 2013). Another study extracted the linear cortical magnification factor in V1 and showed a relationship to individual Vernier acuity thresholds across individual participants. Performance in the acuity task increased as the cortical magnification factor increased, suggesting a direct relationship between visual field representations and visual perception thresholds (Duncan and Boynton, 2003). These studies suggest a direct relation between structural measures of V1 and perceptual differences. Relating behavioural performance with structural measures provides a good starting point in inferring a relationship between brain and behaviour. In an fMRI experiment, Smittenaar et al. (2016) measured V1 with wide-field (37.5 °) population receptive field (pRF) mapping in deaf and hearing participants. The study reported that deaf adults have larger pRF sizes and thinner cortex within the peripheral representation of V1. Furthermore, the study correlated these visual acuity measures in three eccentricity conditions, and found that deaf individuals were significantly better than hearing within the peripheral condition (20 °). This result did not correlate with the peripheral differences found in V1. In contrast, the acuity results of all participants within the 10 ° condition did correlate with cortical thickness measures. Another study which divided structural measures based on the section of the visual field represented was carried out by Codina et al. (2011). The researchers investigated the retina of deaf and hearing individuals using optic coherence tomography (OCT). Portions of the retinal nerve fibre layer (RNFL) containing projections from the peripheral retina were significantly thicker in deaf participants (Codina et al., 2011). The RNFL thickness within both hearing and deaf participants correlated directly with behavioural measures of peripheral visual field sensitivity in both the far-peripheral (60 °) and near-peripheral (30 °) conditions. These studies both provide evidence of early-

visual structural differences of the retina relating to visual processing advantages specific to the near and far-peripheral visual field. In a similar fashion, the aim of the current comparisons were to match structural measures from representations in primary visual cortex with the corresponding parts of visual field involved in the motion tasks. Both global and local motion tasks were correlated with V1 measures.

6.3.1 Global Motion Discrimination

It was hypothesised that better performance in the peripheral global motion discrimination condition would be facilitated by a larger V1 surface area representing the far-periphery. Faster reaction times and lower thresholds would be expected in line with a larger peripheral visual field representation. Likewise, larger central visual field representations in V1 were expected to coincide with faster reaction time and lower thresholds in the central global motion discrimination task. This comparison used measures of the central global motion discrimination condition, which included motion in an aperture 5 ° in radius around fixation. The performance of each subject in this condition was correlated with their central structural surface area of V1, encapsulating 0-15 °. The peripheral global motion condition, which included motion between 40 °- 89 °, was correlated with the far-peripheral region of V1 covering 40 °-72 °. Nine hearing and twelve deaf individuals completed these experiments, and all and were included in these comparisons. As no significant differences were seen between the deaf and hearing participants within the behavioural thresholds or reaction times in the above mentioned conditions, all participants were included in the same group in these tests. The correlations can be seen in Figure 6.1. The comparison between the V1 far-peripheral (40-72 °) visual field representation and far-peripheral global motion discrimination were not significantly correlated for either threshold (r= -.108, p=.642, n=21) or reaction time (r= .373, p=.096, n=21). Likewise, there was no correlation between the central visual field representation (0-15 °) of V1 and central global motion central threshold (r=.114, p=.624, n=21) or reaction time (r= -.101, p=.664, n=21). These results suggest that the size of cortical surface area representing the visual field corresponding to the visual field location of the global motion discrimination task does not directly facilitate behavioural outcomes of motion discrimination thresholds or faster reaction times.

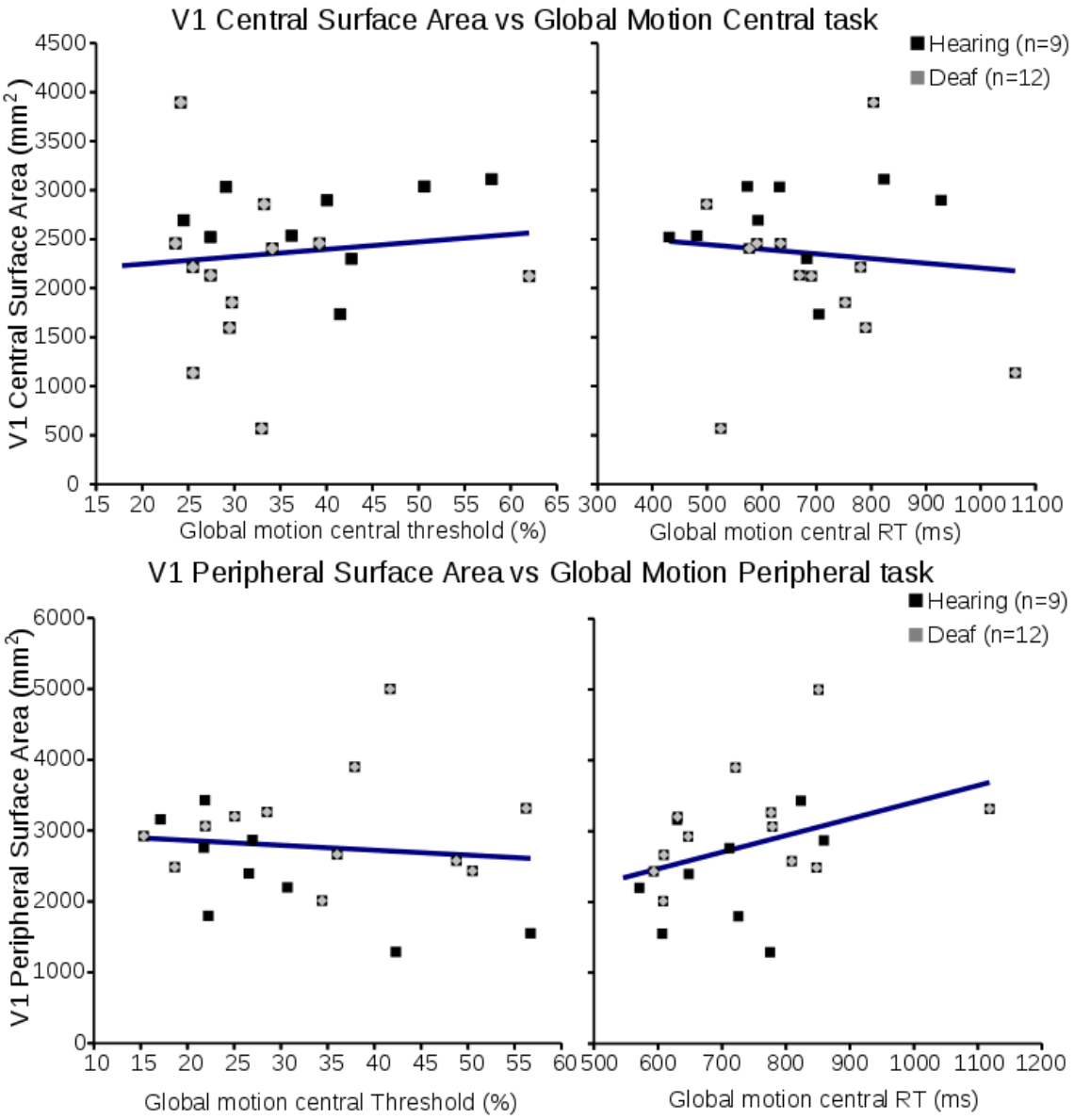

Figure 6.1 – Global motion performance correlated with V1 surface area. The top figures show V1 central representation correlations with central global motion performance, and the bottom two figures show the correlation of the peripheral V1 surface area with peripheral global motion performance, threshold (on the left) and the mean of the median reaction times (on the right) for both pairs. The global thresholds and reaction times were averaged across the left and right peripheral conditions in each participant. In all graphs, each point represents an individual participant (black= hearing, grey= deaf)

6.3.2 Local Motion Detection

The global motion task involves the integration of motion over a wider field, in comparison to previous motion detection measures which show advantages in deaf individuals, such as visual acuity (Smittenaar et al., 2016) or Golmann perimetry (Buckley et al., 2010) where further eccentricities are involved. Direction discrimination is a motion computation performed within motion area V5/MT+, rather than in V1 (Heeger et al., 1999). Neurones selective for direction discrimination of motion in this area have been identified in a number of electro-physiological studies (Bartels et al., 2008; Maunsell and Newsome, 1987). Therefore, a second task involving more localised detection of motion was employed in the current investigations. It was hypothesised that larger peripheral, mid-peripheral and central surface area in V1 representations would facilitate better behavioural performance, lower thresholds and faster reaction times, within the local motion detection task located in the corresponding region of the visual field. Here, the measures compared included the local motion task, namely: behavioural outcomes from the 5 ° and 10 ° conditions which were compared with the central visual field representation, the performance in the 20 ° condition with the mid-peripheral V1 division, and the 40 ° condition with the far-peripheral V1 region. Seven hearing and eleven deaf individuals completed these tasks and were included in these comparisons. These results can be seen in Figure 6.2. The thresholds and reaction times for the 5 ° and 10 ° eccentricity conditions were not significantly different from each other (see Chapter 5, section 5.6.3) and were averaged to make these measures better matched with the central visual field region defined (0-15 °). As no significant differences were seen between the deaf and hearing participants within the behavioural thresholds or reaction times in the above mentioned conditions, all participants were included in the same group in these tests. No significant correlation was found between the central visual field representation of V1 with threshold (r=.053, p=.830, n=19) or reaction time (r=-.160, p=.513, n=19). The mid-peripheral (15-40 °) visual field representation did not correlate with the 20 ° local motion detection thresholds (r=.267, p=.270, n=19) or reaction times (r=.177, p=.469 n=19). Finally, the surface area of the far-peripheral (40-72 °) representation of V1 was not significantly correlated with the 40 ° local motion detection threshold (r=.174 p=.489, n=18) or reaction time (r=.225, p=.369 n=18).

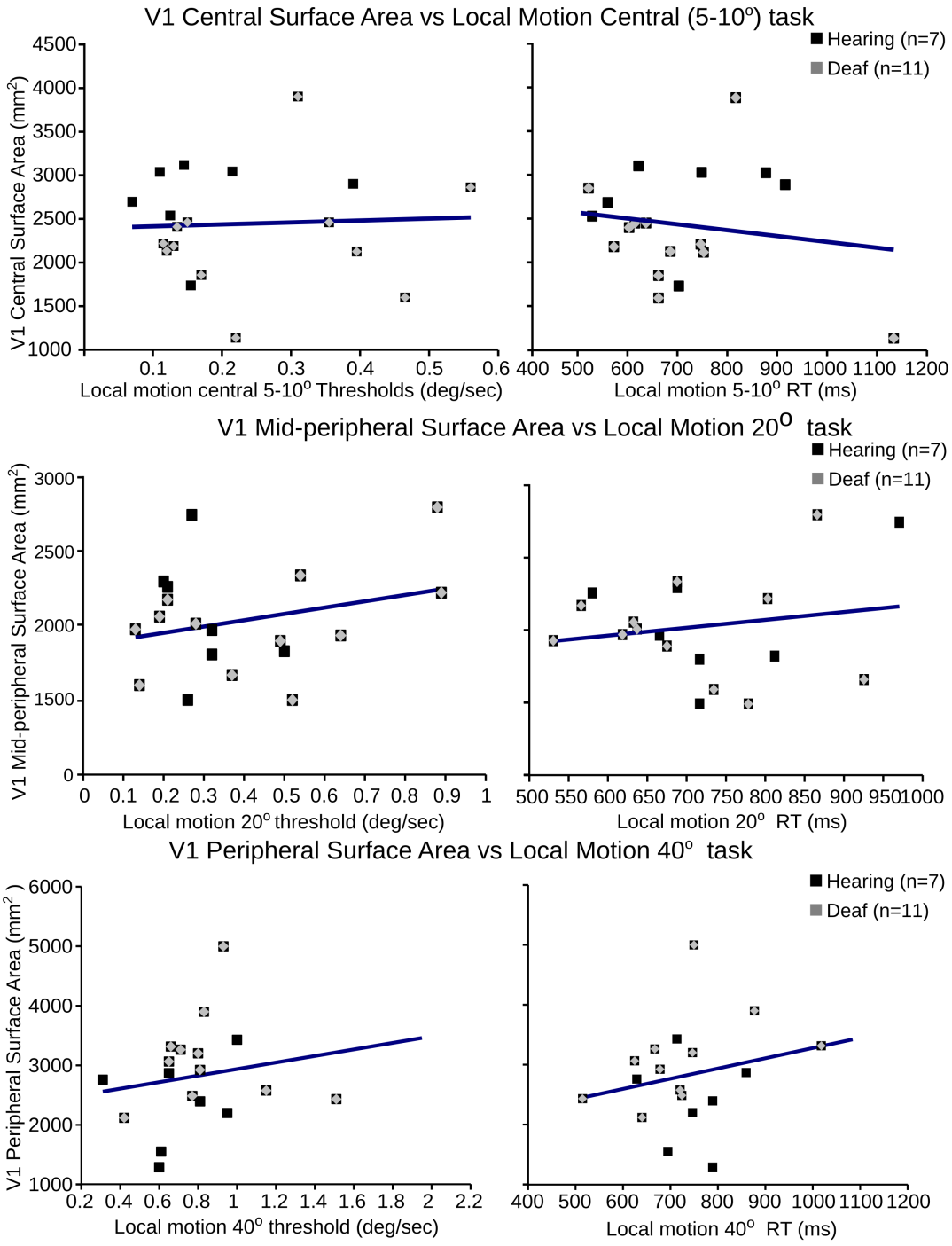

Figure 6.2 – Local motion performance correlated with V1 sub-ROI surface area. The top figures show V1 central representation correlations with central local motion performance, the middle figures the mid-peripheral representation of V1 with the mid-peripheral local motion condition, and the bottom two figures show the correlation of the peripheral V1 surface area with peripheral local motion performance. Thresholds are given on the left and the mean of the median reaction times are givenon the right for all three pairs. In all graphs, each point represents an individual participant (black= hearing, grey= deaf)

6.3.3 Discussion of Structural Measures and Motion Processing

The cortical surface areas of respective visual field representations do not directly relate to behavioural outcomes in the global motion discrimination or local motion detection tasks. It is known that primary visual area V1 is not a region specialised in motion processing, but does relay the signal on to motion processing areas. It is possible that in the case of the local motion detection results in the current study, and previous studies of Vernier acuity (Duncan and Boynton, 2003) or strength of visual illusions (Schwarzkopf and Rees, 2013), the cortical representation does influence perception, as stimuli are static and the resolution provided by a larger cortical representation had an effect here. In light of the local motion detection task, even though the displacement of the stimuli was very small, the task may rely more on motion processing signals which are compiled further down the visual stream. Here, magnification differences may not play a crucial part. Global motion discrimination on the other hand contains large fields of motion, and relies on different motion processing mechanisms. These mechanisms are more in line with neuronal properties seen in motion area V5/MT+, such as its sensitivity to motion direction (Heeger et al., 1999). Therefore, it is possible that it is the processing of relayed information further downstream which leads to behavioural differences, and possible correlates of visual motion performance. Larger emphasis of the periphery does not necessarily indicate faster processing or heightened sensitivity. Smittenaar et al. (2016) found larger pRF sizes in deaf participants within the extent of V1 they tested (37.5 °), and suggested that these might show a greater overlap and lead to better performance in acuity measures. The study also discusses that smaller pRF sizes would demand larger cortical surface, but did not believe this to be the case in their data. Considering the present study, it is possible that pRF size does not increase as rapidly in deaf as it might in hearing individuals as one progresses into the periphery, and this is why the cortical surface area representing the far-periphery in deaf individuals is larger (as seen in Chapter 3). Receptive field sizes are too small in early visual areas to incorporate longer-range interactions between stimuli, such as those needed to integrate across the larger regions of dot motion required in the global motion tasks. Receptive fields in early visual areas are smaller than those seen further down the visual stream, and increase in size with eccentricity (Harvey and Dumoulin, 2011; Amano et al., 2009; Dumoulin and Wandell, 2008) (see Figure 6.3), which would suggest that possible substrates of visual motion processing are facilitated by extrastriate regions

such as V5/MT+ (Pascual-Leone and Walsh, 2001). These later regions are characterised by larger receptive-field sizes, where subregion TO-1/MT in non-human primates contains a very large proportion of direction selective neurons (Ungerleider and Desimone, 1986). Primate area TO-2/MST shows much larger receptive fields than those seen in area TO-1/MT, which it receives signals from. In addition, the local motion task did not extend further than 40 °. The motion task requiring participants to detect if motion was present in the right or left hemifield aperture was constrained by screen size, such that the extent of the visual stimulus was limited to 40 ° in each hemifield. The difference in surface area between hearing and deaf participants was, however, at its largest beyond 40 ° (Chapter 3). This also corresponds to previous literature, where the greatest differences in motion sensitivity have been found at further eccentricities (Buckley et al., 2010; Lomber et al., 2010). Future investigations could incorporate conditions extending beyond those eccentricities tested here.

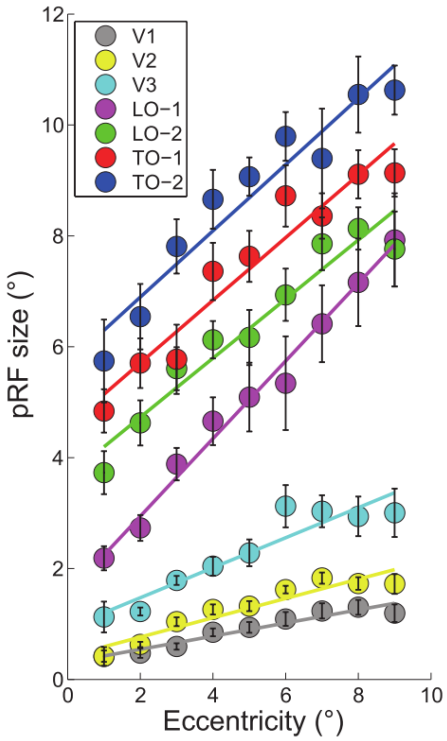

Figure 6.3 – A graph from Amano et al 2009 showing averaged pRF sizes as a function of eccentricity for the visual field maps identified in their study. The pRF size increase from V1/2/3 to LO-1/2 and TO-1/2 (MT/MST). In each visual area, pRF size increases linearly with eccentricity.

6.4 Part 2: Functional Measures and Behaviour

Are responses in visual motion processing regions related to motion processing task performance?

Bavelier et al. (2001) found a higher extent of activation within motion area V5/MT+ in deaf individuals, but could only speculate on whether it provides the neural substrate behind heightened visual motion processing advantages observed in behavioural studies (Stevens and Neville, 2006; Buckley et al., 2010; Hauthal et al., 2013b; Shiell et al., 2014). No previous studies have made direct comparisons between the modulation of the visual motion area V5/MT+ and visual motion performance measures in deaf individuals. The aim of the present comparisons was therefore to investigate the relation between cortical activation to wide-field optic flow motion (72 °) and a closely matched wide-field motion discrimination task. Additionally, no previous studies have investigated activation of motion area V6 in relation to visual motion performance. This region is of particular interest in the current study, as it shows a large peripheral visual field emphasis, and is particularly active during ego-centric optic flow motion (Cardin and Smith 2011; Smith et al., 2006; Pitzalis et al., 2006; Galleti et al., 1999). Thus the global motion processing task was specifically designed to target area V6, and V5/MT+. Activation of V5/MT+ was compared with central and peripheral motion processing performance, as the area encapsulates sub-regions which are functionally distinct and process central, as well as peripheral motion. V6 activation was only compared to peripheral global motion task performance, as the area shows a less magnified representation of the central visual field and a large peripheral emphasis compared to earlier visual areas (Pitzalis et al., 2006), Here, there were no predictions as to its specific involvement in possible advantages in central global motion processing in deaf individuals.

6.4.1 Global Motion Discrimination

In line with the outlined literature, this study hypothesised that neural responses in motion processing visual regions V5/MT+ and V6 could serve as correlate in global motion task performance. It was hypothesised that higher responses in these cortical regions would be negatively correlated with lower motion detection discrimination thresholds and shorter reaction times. Twenty-one hearing and twelve deaf individuals were included in these

comparisons, and signals in V5/MT+ and V6 represent the percent signal change in the BOLD response to a whole field coherent optic flow motion stimulus. Signals seen in V5/MT+ were averaged across hemispheres and hemifield conditions as there were no significant differences seen between them, as can be seen in Chapter 4. V6 activation was extracted across contralateral coherent motion activation, and averaged, as previous studies show that V6 displays a full contralateral hemifield representation (Pitzalis et al., 2006). Behavioural measures of reaction time and threshold in the global motion task were collapsed across hemifield conditions as no significant differences were seen between these (see Chapter 5). As no significant differences were seen between the deaf and hearing participants within the behavioural thresholds or reaction times in the global motion discrimination task, all participants were included in the same group in these tests. The results for V5/MT+ are displayed in Figure 6.4. V5/MT+ activation to wide-field optic flow motion stimuli did not correlate significantly with thresholds within the central global motion discrimination task ($r = -.041$, $p=.822$, $n=33$). Furthermore, there was no significant correlation found with the reaction times ($r= -.302$, $p= .087$, $n=33$), although trends are in the expected direction (higher V5 activation is associated with faster reaction times). Neural activation of V5/MT+ to wide-field optic flow motion stimuli did not show any significant correlations with peripheral global motion thresholds either, as can be seen in Figure 6.4 ($r=-.242$, $p=.175$, $n=33$) the neural responses did not correlate significantly with reaction times either ($r=-.206$, $p=.251$, $n=33$), although trends are in the expected direction (higher V5/MT+ activation is associated with lower thresholds). The results for V6 are portrayed in Figure 6.5. Correlations of V6 modulation by wide-field optic flow motion stimuli did not yield any significant correlations with the peripheral global motion thresholds ($r=-.036$, $p=.843$, $n=33$) or reaction times ($r=-.007$, $p=.968$ $n=33$). The results do not indicate any significant relations between the recruitment of motion area V5/MT+ and observed task performance in global motion discrimination within the far-periphery and central visual field. The same was apparent in V6 activation, which did not show any facilitation in relation to peripheral global motion performance.

6.4.2 Discussion: Global Motion and Visual Motion Areas

No significant correlations were observed between visual motion areas V5/MT+ and V6 with measures of global motion performance. However, there is a possible trend within the

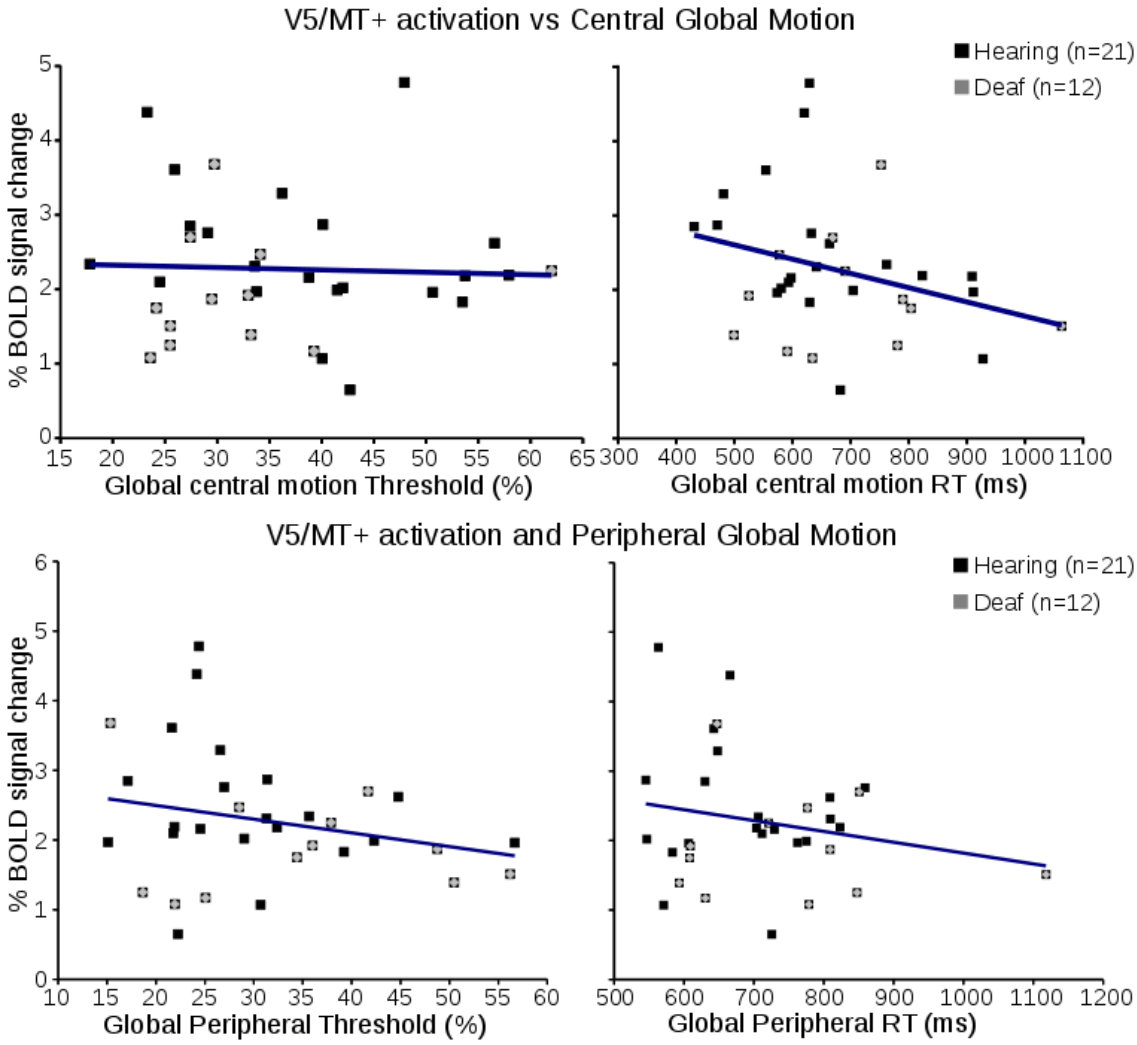

Figure 6.4 – The top figures show neural activation in V5/MT+ against central global motion performance, and the bottom two figures show the correlation neural activation in V5/MT+ with peripheral global motion performance. Thresholds are shown on the left and the mean of the median reaction times are shown on the right for both pairs. Activation in V5/MT+ was averaged across hemispheres and hemifield runs. The global thresholds are averaged across left and right peripheral conditions in each participant. In all graphs, each point represents an individual participant (black= hearing, grey= deaf).

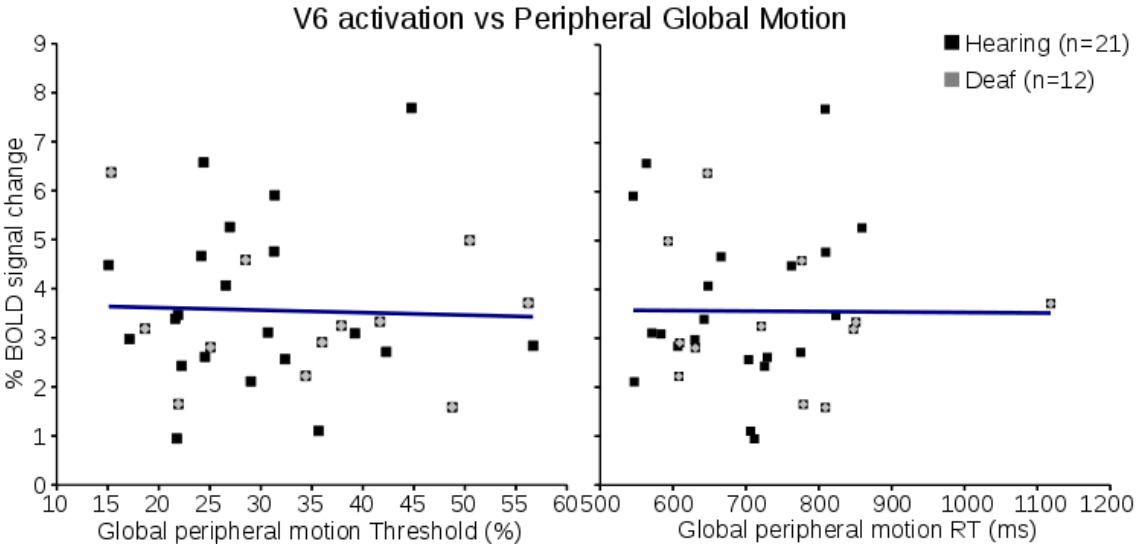

Figure 6.5 – Contralateral activation to coherent motion in V6 is averaged across hemispheres. The global thresholds and reaction times were averaged across the left and right peripheral conditions in each participant. The graphs show the neural activation in V6 against peripheral global motion performance. Thresholds are given on the left and the mean of the median reaction times (on the right). In all graphs, each point represents an individual participant (black= hearing, grey= deaf).

correlation of central global motion reaction times and the activation seen in V5/MT+. The broad definition of V5/MT+ includes MT, MST, and FST (Kolster et al., 2010), and in humans, MT and MST are identified as subdivisions TO-1 and TO-2 (Huk et al., 2002; Amano et al., 2009). These regions show functional differences, and the responses included here are averaged over the extent of all three sub-regions. Motion processing models suggest that motion perception is led by the relative difference between neural responses of neurones with different direction preferences (Simoncelli et al., 1998). Neuroimaging evidence from fMRI does show direction-selective interactions in area V5/MT+ to motion opponency (Heeger et al., 1999). The trend seen in the current data may suggest that greater activation of V5/MT+ is related to faster judgements of motion direction, where the average activation is driven by stronger responses of neurones tuned to the direction of the observed coherent motion. It is possible that TO-2 could be more involved in integrating global motion, as it has larger receptive fields (Amano et al., 2009) as required by the peripheral global motion task. However, responses from the multiple functional regions MT/TO-1, MST/TO-2 and possibly FST (as found in non-human primates, Ungerleider & Desimone, 1986) making up the V5/MT+ area could cancel out at the spatial resolution

possible with fMRI, or there may be an interaction of regions where one is responsible for suppressing irrelevant motion signals, whilst others extract relevant ones. However, as this study extracts activation averaged across a broad selection of V5/MT+, it is difficult to dissociate which subregions of V5/MT+ are involved in the activation seen in the current results. More focal ROI localisers would be needed to dissociate the involvement of each sub-region of V5/MT+ to potentially assess how the activation in these subregions is related to task performance (e.g. Kolster et al., 2010). Even though V6 possesses a large peripheral emphasis and is activated by wide-field optic flow motion (eg. Pitzalis et al., 2006; Cardin et al, 2012, also see Chapter 4), it does not seem to mediate task performance in the global motion discrimination task examined here. Therefore, even though V6 does not appear to be involved in the heightened sensitivity observed in deaf individuals, at least as measured here, it is a visual region and could possibly facilitate other behavioural advantages requiring a wide peripheral representation, which have not been explored in this study. Some studies indicate that V6 is involved in segregating visual objects out of moving backgrounds and the processing ego-centric motion (Pitzalis et al., 2013). Furthermore, V6A is a visual area adjacent to area V6 (Galletti et al., 1999) and it contains cells displaying reach-related activity (Fattori et al., 2009b). As a non-human primate study of grasping movements made in darkness found, V6A is engaged in the online control of reach-to-grasp movements and subtracting motion occurring within reachable distances from more global motion (Fattori et al. 2009). So, even though the area has strong peripheral representations, it is possibly not involved in heightened behavioural perception within tasks such as far-peripheral motion discrimination as investigated here, or tasks seen in previous literature (Buckley et al., 2010). If V6 was served as a neural substrate of peripheral motion processing, it would likely involve tasks within which deaf individuals might be better at extrapolating a target within motion fields. von Pföstl et al. (2009) investigated responses recorded using magnetoencephalography (MEG), where their data suggests a connection between V1 and V6, as the latency of response in V6 was not significantly different from V1. It is possible that V6 supplies signals to the medial dorsal stream, and is involved in the processing of visual motion in line with visually guided actions.

Are responses in cross-modal motion processing regions of auditory cortex related to motion processing task performance?

Cross-modal plasticity and the recruitment of auditory regions in heightened visual motion processing has been shown in congenitally deaf cats (Lomber et al., 2010, Meredith et al., 2011). In deaf humans, multiple regions in auditory cortex are active during peripheral visual perception, and the processing of tactile stimuli, suggesting crossmodal recruitment (Fine et al., 2005; Bavelier et al., 2006; Finney et al., 2001; Levanen et al., 1998; Scott et al., 2014). However, possible perceptual advantages facilitated by cross-modal activation are not clear, as there are only a handful of studies which attempt to relate the structure and recruitment of auditory cortex to perceptual advantages. Shiell, Champoux and Zatorre (2015) found cortical thickness of the right planum temporale (PT) was greater in deaf participants with better visual motion detection thresholds. Another example was Shiell and Zatorre (2016), who found that higher diffusivity in the right PT correlated with worse thresholds, while higher fractional anisotropy correlated with lower motion detection thresholds in deaf individuals. An fMRI study investigated brain responses in deaf and hearing individuals to global motion and form-from motion. Here, higher response amplitudes were seen in the deaf group within secondary auditory regions when compared to hearing participants (Vachon et al., 2013). Another recent fMRI experiment investigating cortical reorganisation included deaf and hearing human participants who were presented with temporally complex sequences of stimuli in the form of visual and auditory rhythms. Deaf and hearing participants carried out the task in the central visual field, while the hearing group also carried out the task in the auditory modality. The posterior lateral part of higher-level auditory cortex was active when deaf participants performed the task visually, and when hearing participants performed it aurally. The study suggests that the task specific function is preserved in auditory cortex, but the input-modality processed has been changed based on the available senses (Bola et al., 2016). This evidence outlines the involvement of auditory cortex in visual processing, however, no studies have investigated subregions of auditory cortex to understand which show the highest levels of plasticity and involvement in supporting advantages in motion perception. Using three subdivisions within auditory cortex, used across the literature, and relating activity within these regions to two different motion perception tasks, the current study was designed to elucidate which aspects of motion processing are facilitated by cross-modal recruitment.

6.4.3 Global Motion Discrimination

As outlined above, studies which have looked at cross-modal plasticity in deaf individuals indicate that auditory regions are recruited for visual motion processing. This study hypothesised that higher neural responses in auditory regions of deaf individuals would correlate with better peripheral thresholds as well as faster reaction times within the peripheral motion tasks. There were no significant differences between deaf and hearing individuals in the visual motion tasks presented in Chapter 5. Here, all participants were included in these correlations to compare individuals on a spectrum. Stronger suppression in hearing individuals could be met with better visual performance, whilst in deaf, stronger activation could indicate cross-modal plasticity and facilitation of visual motion performance. Both global motion discrimination and local motion detection in the central and peripheral visual field extent were compared with auditory activation. As no significant differences were seen between the deaf and hearing participants within the behavioural thresholds or reaction times in the global motion discrimination task conditions, all participants were included in the same group. Responses within the previously described regions of auditory cortex (Chapter 4), the Planum Temporale, Heschls Gyrus and area Te1.2, were correlated with reaction times and thresholds of both motion tasks. Twenty-one hearing and twelve deaf individuals were included in these comparisons, and signals in auditory regions represent the percent signal change in the BOLD response. The signals consisted of the averages across hemifield runs and hemispheres to provide a neural measure for optic-flow motion across the whole visual field. Many comparisons were made, and the reported statistical values for the following correlations are uncorrected for multiple comparisons. The central global motion discrimination thresholds was not significantly correlated, however possibly trending towards a negative correlation with neural responses in area PT ($r=-.357$, $p=.042$). The peripheral global motion threshold of all participants showed a possible trend towards a positive correlation with neural responses in area Te1.2 ($p=.010$). These results can be seen in Figure 6.6. No other responses in any auditory region showed any possible trends with either threshold or reaction time measures within the central or peripheral global motion discrimination task (see Table 6.1). The trend seen in the results suggests that the higher the activation in area PT, the lower the central thresholds are. Region Te1.2 on the other hand, suggests that the more suppressed the signal is here, the better the perceptual threshold is in the peripheral task.

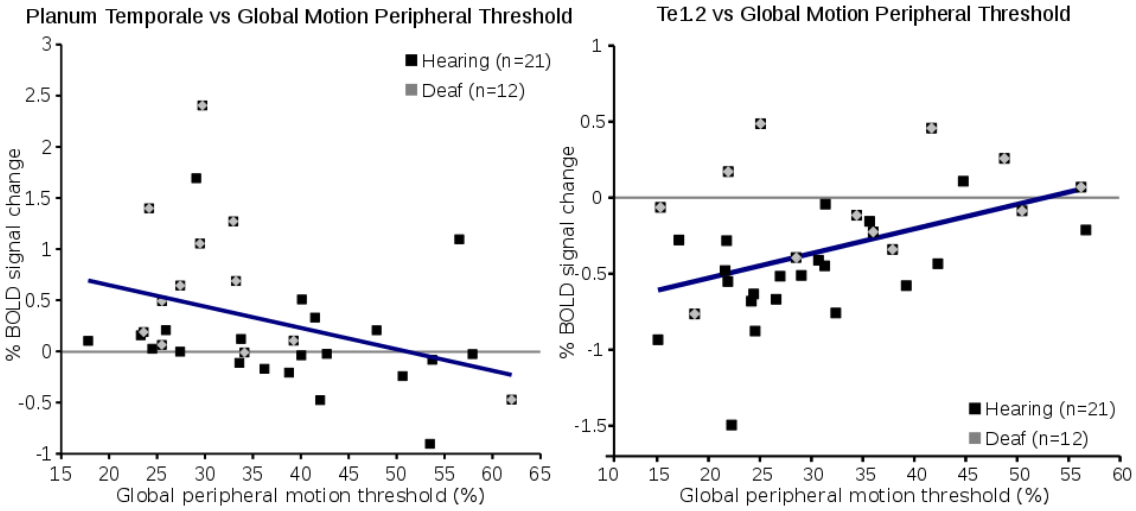

Figure 6.6 – The global thresholds were averaged across the left and right peripheral conditions in each participant. The graphs show the neural activation in the PT and Te1.2 against peripheral global motion performance. In all graphs, each point represents an individual participant (black= hearing, grey= deaf).

Table 6.1 – Pearsons correlation results between auditory regions and global motion discrimination thresholds and reaction times. Note that none of the results are significant, as the tests are not corrected for multiple comparisons.

Thresholds	Global Central (n=33)	Global Peripheral (n=33)
Planum Temporale	R=-.357, p=.042	R=.044, p=.806
Heschl's Gyrus	R=-0.253, p=.155	R=.261, p=.142
Te1.2	R=-.223, p=.213	R=.440, p=.010

Reaction Times	Global Central (n=33)	Global Peripheral (n=33)
Planum Temporale	R=.101, p=.575	R=.144, p=.425
Heschl's Gyrus	R=-.002, p=.992	R=.178, p=.323
Te1.2	R=-.056, p=.759	R=.108, p=.550

Table 6.2 – Pearsons correlation results between auditory regions and local motion discrimination thresholds and reaction times. Note that none of the results are significant, as the tests are not corrected for multiple comparisons.

Thresholds	Local Central 5-10 (n=28)	Local 20 (n=28)	Local 40 (n=27)
Planum Temporale	R=.049, p=.806	R=.157, p=.425	R=-.207, p=.301
Heschl's Gyrus	R=.328, p=.088	R=.386, p=.043	R=-.086, p=.670
Te1.2	R=.205, p=.295	R=.319, p=.098	R=-.079, p=.694

Reaction Times	Local Central 5-10 (n=28)	Local 20 (n=28)	Local 40 (n=27)
Planum Temporale	R=.135, p=.493	R=.168, p=.392	R=-.241, p=.225
Heschl's Gyrus	R=-.037, p=.851	R=-.043, p=.829	R=-.332,p=.090
Te1.2	R=.010, p=.961	R=-.068, p=.723	R=-.138, p=.493

6.4.4 Local Motion Detection

Correlation with the local motion detection task included 16 hearing and 12 deaf participants. The neural responses to coherent motion within Heschl's Gyrus were averaged across hemispheres in each participant. Many comparisons were made, and none of the reported correlations survived corrections for multiple comparisons. The data showed a possible trend towards a positive correlation between HG activation and the 20 ° eccentricity condition thresholds (r=.386, p=.043, n=28, see Figure 6.7). There were no significant correlations, or trends towards these seen between neural responses of any auditory region with thresholds or reaction times with the local motion detection conditions (Table 6.2). The data suggest that the more Heschl's Gyrus is suppressed, the better participants perform in the local motion 20 ° task.

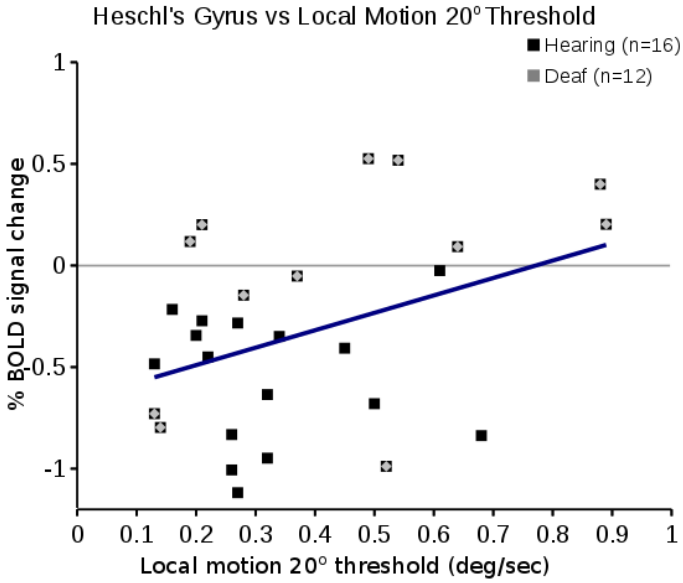

Figure 6.7 – The local motion threshold was averaged across runs in each participant. The graphs show the neural activation in HG against local motion performance. In all graphs, each point represents an individual participant (black= hearing, grey= deaf).

6.4.5 Discussion: Global and Local Motion and Auditory Areas

To summarise, the task performance showed possible trends with auditory regions, where stronger suppression of area Te1.2 could be related to lower peripheral global motion thresholds, and stronger suppression in HG could influence higher sensitivity (lower thresholds) in the local motion 20 ° condition. In contrast, the recruitment in PT showed a trend in promoting better thresholds in the central visual field for global motion discrimination. Differences between the recruitment of auditory regions between deaf and hearing individuals have been noted before (Fine et al., 2005; Karns et al., 2012; Scott et al., 2014), however only in some of these cases have these measures been related to behavioural visual performance. The data presented here shows a possible interaction between suppression and activation of particular regions of auditory cortex. Previous studies have shown the involvement of the PT in spatial auditory processing in hearing individuals (Griffiths et al., 1998; Baumgart et al., 1999), and the current data suggest that the function of this area is preserved in deaf individuals, but the input modality is instead visual. Here, the trending correlation is only specific to the central global motion condition, and no effect is seen in the global peripheral or local motion 40 ° condition. It is interesting to note that the neural responses in the PT did not correlate with the central local motion task thresholds, but

did show a possible trend with the central global motion thresholds. This indicates that cross-modal modulation of the PT might facilitate the extraction of motion from noise, rather than just the detection of movement. The primary auditory region, HG, appears to be suppressed in order to facilitate motion processing thresholds. It is possible that more secondary regions become active, whilst primary regions which show less plasticity need to be suppressed when cross-modal processes are involved in motion processing. This is also true of the more anterior region Te1.2, where suppression is also needed for better motion thresholds in peripheral global motion.

6.5 General Discussion

These comparisons do not provide evidence that V1 surface area mediates thresholds or reaction times in the specific motion tasks studied here. Neural activity in visual motion areas V5/MT+ and V6 do not show direct involvement in motion task performance either. Neural responses in auditory regions however, do show possible trends relating to motion processing thresholds, but not reaction times. Suppression in the PT and Te1.2 regions and activation in HG show a possible relation to better motion perception thresholds. Differences between deaf and hearing individuals in cortical V1 surface area distribution relative to eccentricity could mediate other behavioural advantages, which this study did not investigate. It is possible that deaf individuals could show advantages in ventral stream tasks but in the periphery, as it seems that the relative representation of the visual field could facilitate static stimulus comparisons, and not necessarily dorsal stream functions, such as motion perception. V5/MT+ is a widely known motion area, and as the main input it receives is visual, it is possible that levels of plasticity here would be limited, as visual inputs are still intact in deaf individuals. V6, despite having a large emphasis on the periphery, does not appear to be involved in the motion processing tasks considered here. As previously described (Chapter 4: section 4.6.2), there do not appear to be differences between deaf and hearing individuals in its modulation either. The auditory regions explored here showed significant effects of cross-modal plasticity. The three regions of auditory cortex displayed distinct patterns of responses in deaf individuals when compared to hearing participants (as seen in Chapter 4). The neural modulation of these regions was related to performance in motion discrimination and detection. Effects of plasticity in deaf auditory cortex therefore seems to promote dorsal stream visual processes, as has

been put forward previously (Armstrong et al., 2002). Vachon et al. (2013) speculate that in deaf individuals, auditory cortex is not involved in shape or motion processing. The current results do not include shape processing, however, and the results presented here could contradict this assumption, as responses in auditory cortex showed possible trends towards predicting motion processing performance. The results described here are amongst the few reported studies making comparisons between brain and perceptual visual performance in deaf human individuals (Bottari et al., 2011; Codina et al., 2011). Further support is provided for cross-modal influences in motion processing seen in deaf individuals, particularly differences between deaf and hearing individuals across auditory regions. Further investigations involving careful identification of subregions of auditory cortex could further disseminate as to which regions show the most plasticity in deaf individuals, and strongest involvement in visual motion processing advantages. The behavioural task used in Codina et al. (2016) combined with neuroimaging methods could provide a useful comparison in identifying regions facilitating faster reaction times in deaf individuals, as well as sign language interpreters. This comparison could further disentangle effects of life-long hearing loss as well as the effect of sign language expertise in hearing individuals. A broader question to ask is what the functional role of heightened motion perception can play in a real life framework, in terms of the ecological relevance of the plastic changes seen in the current study. If auditory inputs constitute fundamental guidance and reorienting of exploratory attention, and the input is lacking in deaf individuals, it is possible that heightened visual sensitivity to peripheral stimuli serve the purpose of compensating to help this guidance system. Therefore, it would be expected that auditory cortical regions could become recruited to perform the same function, but based in the visual modality, triggering orienting responses.

In summary, the comparisons described above do not provide evidence that uni-modal plasticity in V1 and visual motion areas V5/MT+ and V6 are involved in visual motion performance, but that cross-modal plasticity in auditory regions shows possible trends in relation to motion processing performance in deaf and hearing individuals.

Chapter 7

General Discussion and Future Directions

7.1 Overview

When a sensory modality is lost early in life, the brain adapts to the change of sensory information available. A vast amount of research has aimed to explain how sensory processing might change whether remaining senses are heightened, or whether other sensory deficits may occur as a result. This prompts the question of where the neural substrates behind these changes in sensory processing can be seen. This thesis aimed to investigate cortical plasticity resulting from auditory deprivation, and to relate behavioural visual motion processing abilities to plastic changes in the brain. Previous work in animal models (Lomber et al., 2010) have been successful in finding neural substrates of heightened visual performance in congenitally deaf cats. The studies described here aimed to identify where plasticity can be seen, and which visual motion processing regions are more plastic than others in order to facilitate behavioural performance in deaf human adults. This approach also makes it possible to relate brain and behaviour, as many studies focus on studying each of these aspects, but often not in relation to each other. The importance of this research lies in detecting and differentiating between sensory compensation and sensory deficits with several measures. This body of work therefore used structural and functional MRI, alongside visual psychophysical experiments. The following chapter outlines the principal findings from this body of work and their wider implications to our understand-

ing of cortical plasticity in early deaf individuals, and neural substrates of visual motion processing performance. Future directions of this research are also considered.

7.2 Wide-field Visual Field Mapping

Deaf individuals show the highest advantages in processes involving the visual periphery. Therefore, a novel methodological approach was developed in order to allow for wide-field mapping of visual field representations. The aim of this was to capture neural signals in the far-periphery, reaching to an eccentricity of 72 ° along the horizontal dimension. Within fMRI research, projecting visual stimuli aimed at the far-periphery is met with challenges, as the visual field is constrained by the size of the scanner bore which poses limitations the size of the projection screen used. Far-peripheral signals were reliably recorded by scanning participants while stimulating each hemifield separately using a wide-field mirror and closer viewing distance. Currently, there are a handful of studies which reach into the periphery using fMRI, but only up to an extent of 60 ° (Pitzalis et al., 2006; Wu et al., 2013; Yan et al., 2011; Greco et al., 2015). Most studies which measure visual field maps with fMRI only measure a smaller proportion of the visual field representation (less than 20 °). Therefore, the current study was to able to map previously uncharted territory within visual cortex. Furthermore, and most importantly, mapping has not been previously carried out to this visual field extent in deaf individuals, where greatest visual plasticity is expected. The development of this wide-field retinotopic mapping methodology was integral in detecting novel cortical differences between deaf and hearing participants in early visual cortex, discussed below.

7.3 Plasticity in Early Visual Cortical Areas

7.3.1 Cortical Volume

Deaf participants showed a trend towards larger cortical volume representing the far-peripheral visual field. Smaller central visual field representations in V1 were also observed, when compared to hearing controls. Previous studies have investigated volumetric differences in visual field maps between deaf and hearing individuals, finding no differences

in volume using retinotopic methods (Fine et al., 2005). However, a study which defined V1 anatomically (Allen et al., 2013) found larger cortical volume in the calcarine sulcus of deaf native signers, relative to hearing non-signers. This difference was not found in comparison to non-hearing native signers. This finding also demonstrates the interaction between sign language experience and auditory deprivation. It is important to consider the interplay between cortical thickness and cortical surface area, as the effects in cortical volume reported in the current body of work were driven by differences in cortical surface area, not cortical thickness.

7.3.2 Cortical Thickness

Previous studies of deaf individuals acquiring sign language either early or late in life showed that late sign language learners had reduced grey matter thickness in V1, compared to deaf early sign language learners (Pénicaud et al., 2013). These findings along with those of (Allen et al., 2013) indicate that a substantial amount of variability within the deaf group can originate from sensory experience, such as the age at which sign language was acquired. As the current study includes quite a heterogeneous group of deaf individuals, the results possibly contain the differences reported by (Pénicaud et al., 2013). No significant differences were found within the cortical thickness measure between deaf and hearing groups in the current data, however these comparisons can incorporate larger sources of variability as sign language age acquisition was not controlled for. Also, studies investigating brain plasticity as a result of congenital and early blindness have found increased cortical thickness within early visual areas (Bridge et al., 2014; Park and Chun, 2009). When a sensory input is not available, it can result in thicker and more immature cortex (Bridge et al., 2014; Jiang et al., 2009). It is likely that deaf individuals show thinner cortex due to a larger demand for higher visual resolution which is met with typical pruning mechanisms during development. Song et al. (2009) found that cortical thickness in V1 showed a negative correlation with sharpness of neural population tuning and perceptual discrimination accuracy at varying visual field positions. Cortical surface area was however positively correlated with neural population tuning and the perceptual discrimination task performance. Their findings indicate that advantages in visual perception are facilitated by an enlarged and thinner cortical surface area in visual cortex.

7.3.3 Cortical Surface Area

The cortical magnification gradients, based on cortical surface area, show a trade-off between the central and far-peripheral representation between the deaf and hearing groups. The increase cortical surface area in deaf participants could have resulted due to a higher demand for higher visual resolution, as suggested by Song et al. (2015). Enlargement of visual cortical surface area could result in more cortical columns, in turn allowing greater selectivity due to sharper neural tuning, leading to better performance in perceptual discrimination in visual tasks.

7.4 Relationship to Visual Performance

However, this difference in cortical surface area does not appear to extend to the behavioural motion tasks used in this body of work. The differences found in surface area in the far-periphery and central representations between hearing and deaf participants did not correlate with motion processing thresholds or reaction times.

7.4.1 Global Motion Task

The global motion discrimination task required the discrimination of coherent signals in incoherent noise over a larger visual field, which V1 is not tuned to, compared to motion area V5/MT+ (Maunsell and Newsome, 1987). This is due to the difference in receptive fields, as well as neural tuning to different directions of motion. Likewise, when investigating coherent and incoherent motion signals in fMRI, Braddick et al. (2001) compared activation in V5/MT+ and V1, and reported that V5/MT+ is selective to coherent motion, when compared to dynamic noise (incoherent motion), whilst V1 showed no selectivity to coherent over incoherent motion. Therefore, it is perhaps not surprising that structural differences in early visual cortex did not show a relation to visual motion processing in the global motion task. If a larger cortical surface area were to facilitate perceptual thresholds and possibly reaction times, one would expect the hearing individuals to perform better in the central global, and more central local motion tasks, which they do not. Interestingly, deaf individuals show a larger representation of the far-periphery, but worse thresholds in

the peripheral global motion task. In deaf participants, Smittenaar et al. (2016) found receptive field sizes to increase in size, but their density remained the same, possibly leading to larger overlaps of these fields leading to better discrimination of peripheral stimuli. There was no evidence of an increased surround representation. These findings may lend themselves more to better performance in visual acuity measures, rather than global motion discrimination. The larger overlaps between receptive fields could possibly lead to a disadvantage in the case of global motion discrimination, which is the case in the current data set where deaf individuals show worse thresholds in the peripheral visual field condition. This might be due to larger number of receptive fields being stimulated by wide-field coherent and incoherent motion stimuli, making it difficult to resolve what direction the coherent dots are moving in.

7.4.2 Local Motion Task

In the local motion detection task, only a small displacement of dots indicates motion, where V1 surface area could potentially facilitate better performance in the local motion task. This was however not seen in the current data, and it is possible that it is the V1 response magnitude which could be related to the performance in the local motion task, rather than the cortical surface area. V1 is not specifically selective to motion direction, like V5/MT+ (Heeger et al., 1999). This is due to different receptive field sizes within these regions V1 has much smaller receptive fields compared to V5/MT+ (Amano et al., 2009), making area V5/MT+ highly likely to be a neural substrate for motion processing when considering these tasks. It is possible that the perceptual advantage offered by the structural difference in V1 are related to other visual advantages, not tested in the current body of work. For example, previous studies demonstrated that performance in acuity tasks requiring high spatial resolution and precise localisation in space were related to the difference observed in visual field representations, as they required the spatial precision provided by small V1 receptive fields (eg. Song et al., 2015; Duncan and Boynton, 2003; Schwartzkopff and Rees, 2013; Smittenaar et al., 2016). The two tasks considered in the current body of work however, converge with the findings of Lomber et al. (2010) where congenitally deaf cats showed a superior ability in detecting motion, but show slightly worse performance in motion discrimination tasks. Nevertheless, cortical surface-area distribution differences observed here do provide novel evidence of plasticity within

the cortical distribution of central and peripheral visual field representations within the primary visual cortex of congenitally deaf adults. The implications of this plasticity remain to be tested, and are discussed further in this chapter.

7.5 Plasticity and Motion Processing Areas of the Brain

When coherent visual motion was presented during fMRI scanning, results showed distinctive differences in response profiles in auditory, but not visual motion, regions of the brain when comparing deaf and hearing participants. The neural responses recorded indicate that regions of heightened visual motion processing seen in deaf individuals might not be located in visual motion regions V5/MT+ or V6, at least using the optic flow stimuli we tested. It is possible that there is an effect of plasticity present within the V5/MT+ complex, namely regions TO-1 (MT) and TO-2 (MST), but the current study is not able to distinguish between possible differences in activation within these sub-regions. Furthermore, when considering these regions as substrates of motion perception, the neural activity in V5/MT+ and V6 did not correlate in motion task performance, in either global motion discrimination or local motion detection. Previous work by Tadin et al. (2011) found that the disruption of V5/MT+ with the use of Transcranial Magnetic Stimulation (TMS) led to improvements in discrimination of large moving stimuli. The authors speculated that the result was caused due to TMS weakening the strength of surround suppression. In this study, the overall lower activation patterns seen in V5/MT+ in deaf individuals could be caused by stronger surround suppression and relate to their weaker performance in more peripheral local motion discrimination conditions and global peripheral motion discrimination. This is however not clear in the current data, as there is no significant relationship between V5/MT+ and motion performance.

7.6 Cross-modal Effects

Shifting to cross-modal cortical regions, the results of the current study provide evidence of significant differences in neural activation within auditory regions in the superior temporal cortex. When comparing deaf to hearing groups, on average there was no positive activation in regions Te1.2 and HG in either hemisphere, however hearing participants

showed significantly stronger suppression when compared to deaf individuals. Higher activation of the Planum Temporale was observed in deaf individuals, especially in the right hemisphere. Previous studies have found that deaf individuals show a higher recruitment of the posterior temporal cortex, which includes the Planum Temporale, in visual processing tasks (Bavelier et al., 2006). This effect was also observed in the current data. When comparing group results such as contrasting neural modulation between deaf and hearing groups, the results could indicate either higher activation in deaf individuals or stronger suppression of neural signals in hearing, therefore resulting in a positive contrast. In the current body of work, these measures are compared between groups and not contrasted. Here, the mean activation in each region is compared between groups against the baseline condition of no motion. This makes it possible to distinguish effects due to suppression, no response, or activation within the subregions of auditory cortex of deaf and hearing participants. Furthermore, this study provides novel findings concerning coherent and incoherent motion perception. Differences between deaf and hearing participants only emerge within coherent motion perception, and no group differences are seen when incoherent motion is concerned. This dissociation has not been reported previously, and is detectable due to the novel approach allowing for wide-field optic flow motion to be presented in fMRI, which provides data never recorded before in deaf or hearing individuals. Interconnections between peripheral visual and auditory regions have been found in non-human primate literature (Falchier et al., 2002). Further studies could explore the neural connectivity between these regions, to explore weather either larger peripheral representations, or larger activation in deaf individuals, could be met with higher activation of secondary auditory regions. These regions show high degrees of plasticity in deaf individuals. Furthermore, this experiment could explore whether this modulation is specific to integrating spatial signals, such as coherent motion, or whether this would be independent of this manipulation.

7.7 Cross-modal Responses and Motion Performance

When relating neural measures to behavioural outcomes, the current study found that neural responses in auditory regions show a possible relationship with motion processing thresholds, but not reaction times; suppression in the HG and Te1.2 regions and activation in PT show trends towards being correlated with better motion perception thresholds in

both deaf and hearing individuals. In hearing individuals, the superior temporal cortex, which contains the auditory regions investigated in the current study, is involved in the integration of auditory and visual signals. It is also involved in multi-sensory illusory percepts such as the McGurk effect (McGurk and Macdonald, 1976), with stronger activation predicting the strength of the perceived effect (Nath and Beauchamp, 2012). This trend indicates the regions possible involvement in multi-sensory integration, and as the region shows plasticity in deaf individuals, it also indicates its ability to adapt to the sensory information available. There is also structural evidence showing white matter differences in the posterior temporal cortex in deaf participants, when compared to hearing controls (Shibata, 2007; Li et al., 2012). Studies have shown reduced connectivity within auditory regions but stronger connectivity between auditory and visual regions in deaf children (Li et al., 2015). These stronger connections could arise due to the larger reliance on cross-modal processing, where the auditory cortex relies more on visual inputs. It is important to consider the described cross-modal findings in line with the observed functional specialisations within the brain. A widely accepted, but more constrained account of brain organisation states that functionally specialised regions of the brain are tied to specific sensory modalities. This idea has recently been challenged, based on evidence that function is preserved in brain regions deprived of normal sensory inputs in congenitally deaf or blind individuals (reviewed in Hemiler et al., 2015). A recent study by Bola et al. (2016) provided evidence that the brain is organised in a task-selective, but sensory independent, manner. When auditory and visual rhythm sequences were presented to deaf and hearing individuals in the sensory modality available to them, the posterior, lateral part of higher-level auditory cortex was activated by the stimuli in both groups. This highlights the flexibility of cortical processing, showing its ability to adapt to different sensory inputs whilst maintaining the computations required to perform specific tasks. In line with this hypothesis, the functional connectivity of the auditory cortex is the same between deaf and hearing adults (Striem-Amit et al., 2016) and deaf cats (Barone et al., 2013). In deaf individuals, this pattern of connectivity may develop in adolescence, after a longer period of sensory deprivation. Li et al. (2015) showed that connectivity within auditory cortex of deaf children is weaker than in hearing, implying that the similarity in connectivity between hearing and deaf adults develops later in life. Collectively, these studies provide support for the concept that sensory input modalities might compete for the recruitment of secondary sensory areas, which are not as specialised as their primary

predecessors. The balance between competing modalities can therefore be shifted in populations which are deprived of a sense (Seymour et al., 2016). This explains the recruitment of secondary auditory cortices to processing visual motion, as seen in the current results. Secondary auditory cortex, normally used for processing spatial auditory signals for the localisation of sounds, might therefore be recruited for processing peripheral visual motion signals. The current study used group atlas templates to define primary and secondary auditory regions. Here, these definitions are approximate, as the boundaries are highly variable between individuals (Morosan et al., 2001). Further investigations could focus on the careful anatomical definitions of the auditory regions on an individual basis (Dick et al., 2012). This could be done by using similar methods used by Glasser and Van Essen (2011) where particular MRI protocols allow for the extraction of myelin content, which in turn helps identify the core and secondary auditory regions based on what is known about the anatomy of these regions (Hackett et al., 2001). The core auditory region is highly myelinated, and the position and profile of the region can therefore be closely matched with post-mortem myeloarchitectonic studies (Morel et al., 1993). Such an approach, with more confident definitions, could further elucidate which regions show the highest levels of plasticity.

In summary, the results of the current study show the possible functional specificity of auditory regions in processing spatial information as a trend towards correlations between visual motion processing performance and neural responses in auditory regions. These findings make novel contributions to the field of brain plasticity, and the debate surrounding possible changes in functional organisation in sensory deprived cortex. The correlation conducted falls on a spectrum rather than in group-defined clusters, leading to the hypothesis that individual differences might be due to variability in sensory experience within the sensory deprived population as well as hearing controls.

Overall, the current data provides evidence of cortical plasticity within sub-regions and different visual representations of space in primary visual cortex, as well as different sub-regions within auditory cortex in response to visual stimuli in deaf individuals when compared to hearing controls. Secondly, a distinction is shown between the neural modulation of auditory regions depending on the motion type observed. Coherent motion reveals the differences between sensory deprived auditory cortex, while incoherent motion does not. These results support the notion that spatial stimuli are integrated in the PT region, al-

beit in response to visual stimuli in deaf individuals. Furthermore, auditory regions are suppressed by hearing individuals during the processing of coherent motion, whilst this is not the case in deaf participants.

7.8 Implications for the Understanding of Auditory Deprivation and Cortical Plasticity

Understanding the neural mechanisms behind functional reorganisation of auditory cortex is crucial given the implications it has upon the successful implantation of cochlear implants and rehabilitation surrounding this process. Understanding which cross-modal functions may or may not persist can better inform decisions on the time at which it would be most beneficial for children to receive a cochlear implant, based on when they have the appropriate neural structures able to process auditory information (Giraud and Lee, 2007). Cochlear implants are usually bilateral, however in cases where unilateral cochlear implants are recommended, understanding lateralisation effects of cross-modal plasticity and functional specificity can inform as to which hemisphere should receive an implant in order for it to be most effective. Previous studies have suggested that, as the right auditory cortex elicits higher activation to visual stimuli, it is perhaps the left auditory cortex which would be better suited in receiving a cochlear implant (Vachon et al., 2013). Evidence of cross-modal recruitment from this and other studies lead to the following important questions: 1) If some regions of auditory cortex are recruited for visual information, would they be able to receive and interpret auditory signals if they were to be restored?, and 2) Do cochlear implants disrupt certain visual perceptual advantages that might have been acquired following loss of hearing and an increased reliance on vision?

7.8.1 Experience Leading to Plasticity

The main motivator for the research described in this thesis surrounds the impact altered sensory experience has, which results in behavioural advantages and cortical plasticity. As has been extensively described throughout, congenital deafness has a profound effect upon peripheral visual processing (eg. Bavelier et al., 2000; Stevens and Neville, 2006; Buckley et al., 2010; Hauthal et al., 2013), and can lead to differential activation, structure, and

connectivity in cortex (e.g. Scott et al., 2014; Bavelier et al., 2000; Lomber et al., 2010, Fine et al., 2005). Behavioural advantages can also be developed through training, and can be seen in non-sensory deprived individuals. Peripheral visual enhancements have been noted in habitual video game players, where there is an improvement seen in their ability to localise peripheral targets amongst distractors (Green and Bavelier, 2003). These individuals also show an extended visual field area (Buckley et al., 2010). Attentional visual enhancements are also seen in athletes, when attentional test stimuli matched their sport (Memmert et al., 2009). These results suggest that extended training of skills which require rapid detection or motor responses to peripheral stimuli can be enhanced, even in hearing individuals. This shows that various forms of training can increase peripheral visual sensitivity, but perhaps not to the same extent as seen in deaf individuals.

7.8.2 Cortical Changes Associated with Behaviour

A clear example of the effects seen following sensory deprivation as well as extensive training was presented by Codina et al. (2016). Congenitally deaf signing participants, BSL interpreters, and hearing non-signers were tested in a far-peripheral visual target detection task. Deaf individuals achieved the fastest response times out of the three groups in far-peripheral locations, and the BSL interpreters were faster than hearing non-signers. The results of Codina et al. (2016) provide clear evidence that sensory training (e.g. in hearing BSL interpreters) can provide modest visual advantages, whilst congenitally deaf individuals, who have had to rely more heavily on vision throughout life, surpass this level and show even stronger perceptual advantages. Researchers in the above mentioned studies have suggested that such differences found between athletes and non-athletes, as well as video game players and non-video game players, might be down to the efficiency with which visuo-attentional pathways are used. This has been described as 'the software' of the system, rather than structural changes, the 'system hardware' (Muiños and Ballesteros, 2013). As mentioned, cortical plasticity has been observed in deaf individuals, within visual and auditory cortex (eg. Scott et al., 2014; Fine et al., 2005; Bottari et al., 2010; Lomber et al., 2010). Large scale organisation can also be seen in non-sensory deprived subjects. An example of this has been demonstrated within the ventral visual cortex, where the Lateral Occipital Cortex (LOC) is recruited for reading Braille in sighted individuals (Siuda-Krzywicka et al., 2016). Higher visual motion area V5/MT+ also shows plasticity

when training involved complex motion processing (Draganski et al., 2004). This is of interest as plasticity has been shown in deaf individuals in V5/MT+ (Bavelier et al., 2000). It is clear that complex learning without sensory deprivation can also lead to some degree of cortical plasticity. In the current study, both hearing and deaf individuals show a correlation between auditory activation and perceptual thresholds of motion processing. This suggests that varying levels of experience with sign language, or other visual tasks involving peripheral processing, can influence performance in the tasks used here. In addition, as discussed above, hearing individuals can also show some signs of plasticity as a result of video game playing, or sports requiring peripheral vision. Although this is the case, the effect of lifelong auditory deprivation still shows the largest effect, both on the neural level (Scott et al., 2014; Fine et al., 2005) and on the behavioural level (Codina et al., 2016; Buckley et al., 2010).

7.9 Implications for Future directions

7.9.1 V1 and Acuity Measures

Future experiments could include investigations of behavioural visual tasks, including those which could elucidate how the enlarged surface area in far-peripheral representations in V1 affect visual performance in deaf individuals. The tasks could include visual acuity judgements, similar to that employed by Smitteenaar et al. (2016) or Song et al. (2015), where deaf participants showed superior performance. Another task could include angular displacement of static stimuli presented in the far-periphery, and because the far-periphery shows a larger representation in cortex, deaf individuals would be expected to detect smaller angles of displacement compared to hearing controls. Tasks such as those employed by Buckley et al. (2010) or Codina et al. (2016), which involve target detection in the far-periphery, would also provide a good measure which has previously shown to be enhanced in deaf. All the above mentioned examples would target the larger far-peripheral representation in V1. Based on previous studies relating the size of cortical representation to visual perception (Duncan and Boynton, 2003; Schwartzkopff and Rees, 2013), the larger representation of the far-periphery may be met with better performance in these measures.

7.9.2 The V5/MT+ Cluster, fMRI and TMS

To further disentangle possible differences between deaf and hearing individuals within V5/MT+, further research could investigate whether activation profiles between deaf and hearing individuals differ between sub-regions of the V5/MT+ complex especially within area TO-2 (proposed human homologue to macaque MST), which integrates over a larger portion of the visual field (Huk et al., 2002). Also, it is possible that previous studies (Bavelier et al. 2001; Fine et al., 2005) report group differences mainly from area TO-1, as the limited visual field stimulated would not incorporate the receptive fields which respond far into the periphery as those of region TO-2. Previous studies have employed effective localiser techniques for fMRI (Strong et al., 2016; Huk et al., 2002), where apertures containing moving dots are shifted by 15 ° to the side of fixation, in either the left or right hemifield. TO-2 can be localised by extracting activation from the ipsilateral hemisphere, whilst TO-1 can be localised by subtracting the activation of TO-2 from the whole V5/MT+ complex during contralateral visual stimulation. These localisers could be used to extract activation from each area when wide-field optic flow is presented. This approach would therefore assess if either of the sub-regions (TO-1 or TO-2) show differential involvement in peripheral global discrimination. Furthermore, as TO-1 and TO-2 would be functionally defined, Transcranial Magnetic Stimulation (TMS) could be applied to these regions during psychophysical testing in the global motion discrimination tasks. Tadin et al., (2011) showed that the disruption of the V5/MT+ complex improved thresholds in visual discrimination of motion, likely due to weakening of the strength of surround suppression. To determine if there is stronger surround suppression in deaf individuals, which may explain their poorer performance on the global motion task, one could test whether disrupting either region with TMS improves their performance thresholds.

7.9.3 V5/MT+ and MEG – Temporal Information

Another avenue worth exploring further includes investigations of neural responses measured by Electroencephalography (EEG) or Magnetoencephalography (MEG). These measures allow for the recording of neural signals on a millisecond scale, providing very precise temporal information of neural modulation. This can complement the higher spatial but poorer temporal resolution of fMRI. It is possible that effects of plasticity in V5/MT+,

which have not been detected in the current study, are exhibited in the neural response time, which fMRI is not sensitive enough to detect. An MEG study carried out by Finney et al. (2003) assessed the neural response times to visual stimulation in deaf and hearing individuals to sinusoidal grating stimuli, appearing in five different locations, including one central and four peripheral conditions (extending to 15 °). They showed right hemisphere responses 100-400ms in auditory cortex of deaf but not hearing individuals. Furthermore, Bottari et al. (2011) showed that response times of deaf individuals were faster in striate cortex, and amplitudes of the P1 complex (100-150ms) were correlated with visual target detection performance. To extend this research, MEG methods could be used to measure responses to the motion stimuli used in the current study (optic flow fields, coherent and incoherent dot motion). In addition, functional localisers could be used to define subregions of V5/MT+, TO-1 and TO-2 in MRI. These localisers could provide virtual electrodes in the MEG analysis to extract the neural time course of the responses within the selected motion regions, and determine whether responses are faster in deaf individuals. It would also be possible to see if any response patterns predict the behavioural measures recorded in the current study. MEG data would also provide novel avenues to investigate the communication between neural regions through functional connectivity analysis, making it possible to see how auditory, visual motion and early visual regions might adapt to a different sensory input. Previous non-human primate studies have shown feedback projections from area MT (TO-1) to peripheral representations in primary visual cortex (Falchier et al., 2002; Shipp and Zeki, 1989). The functional connectivity between these regions could be investigated using MEG in deaf individuals. This could answer questions of potential differences in response time between deaf and hearing groups, as a result of sensory deprivation.

7.9.4 V6, V6A and Other Motion Sensitive Regions

Visual area V6 did not show any correlations with visual motion processing performance, and no differential activation between deaf and hearing participants. Cardin et al. (2012) suggest that V6 could be involved in processing egocentric optic-flow motion in order to help segregate and avoid obstacles in near personal space (Warren and Rushton, 2009). Therefore, even though V6 does not appear to be involved in the heightened sensitivity observed in deaf individuals, it could possibly facilitate other behavioural tasks requiring a

wide peripheral representation, which have not been explored in this study. From an ecological perspective, deaf individuals cannot be prompted to possible dangers by auditory inputs. Therefore, higher activation in V6 could provide a signal to detect hazardous objects within self-motion as deaf individuals move through their environment. However, the current study tested large-field global motion rather than object-from-motion detection specifically.

Another future venture could include applying EEG/MEG in a similar paradigm. Combining this with structural MRI and fMRI localisers for areas V5/MT+, V6 and V3A would allow for source localisation analysis in EEG/MEG (Di Russo et al., 2005). This approach would elucidate any effects of plasticity in relation to the response latencies and amplitudes. Furthermore, involving the same wide-field optic flow stimuli would be beneficial in studying the sequence of activation which can be seen in visual far-peripheral motion processing in deaf individuals. von Pföstl et al. (2009) conducted an MEG study with hearing individuals, looking specifically at neural responses in V6. The study found that responses in V6 occurred in very near temporal proximity to those of V1, predominantly within the cortical source representing the peripheral visual field, whilst temporal occipital regions showed a delayed response onset in comparison to V6. Alongside V6, it would also be beneficial to explore visual area V3A, which is adjacent to dorsal V3, as this visual region is activated by moving stimuli, particularly by first order motion (Tootel et al., 1997; Smith et al., 1998). Pitzalis et al. (2013) investigated motion responses with high-resolution EEG, and found that V3A was activated more by incoherent than coherent motion, in contrast to areas V5/MT+ and V6, which showed higher activation to coherent motion stimuli. As Bottari et al. (2010) investigated visual responses in cortex with EEG, and found signs of plasticity in the C1 and P1 complex, the approaches outlined above could indicate if motion processing in deaf individuals is met with faster cortical responses which are not detectable with fMRI.

7.10 Conclusions

Taken together, the findings reported in this thesis show that congenital deafness in humans leads to plastic changes within primary visual cortex. These findings also show that auditory regions are recruited differentially between deaf and hearing individuals, depend-

ing on which motion type is presented. This activation shows a trending relation with visual motion performance in all participants tested. Possible future directions were discussed to further explore the temporal dynamics of the plastic changes seen, and possible visual tasks which could be facilitated by the effect measured in V1.

Appendix A

Appendix

A.1 Each Step Frame of the Retinotopic Stimuli Used

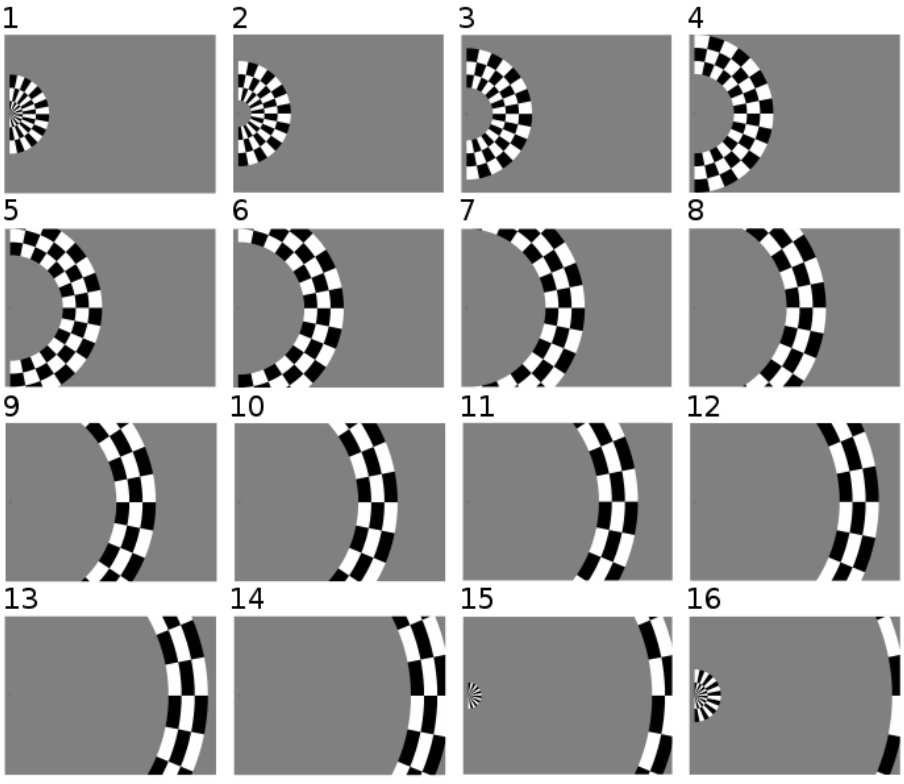

Figure A.1 – All frames representing the 16 steps of the expanding ring frames used to map the right hemifield. Each hemifield was tested separately, with the fixation cross placed 36 °on either the left or right side of the screen. All stimulus counterphase-flickered at 4 Hz and extended from fixation to 72 ° of visual field angle. The stimuli are based on the original retinotopic mapping stimuli used by Wandell et al. (2007).

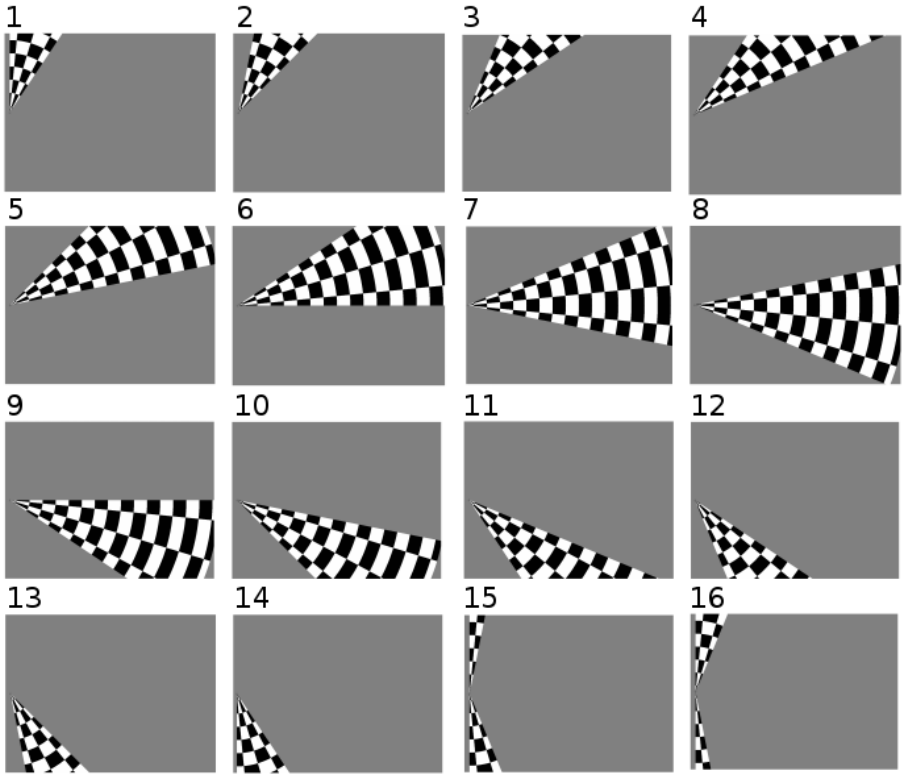

Figure A.2 – All frames representing the 16 steps of the expanding ring frames used to map the right hemifield. Each hemifield was tested separately, with the fixation cross placed 36 °on either the left or right side of the screen. All stimulus counterphase-flickered at 4 Hz and extended from fixation to 72 ° of visual field angle. The stimuli are based on the original retinotopic mapping stimuli used by Wandell et al. (2007).

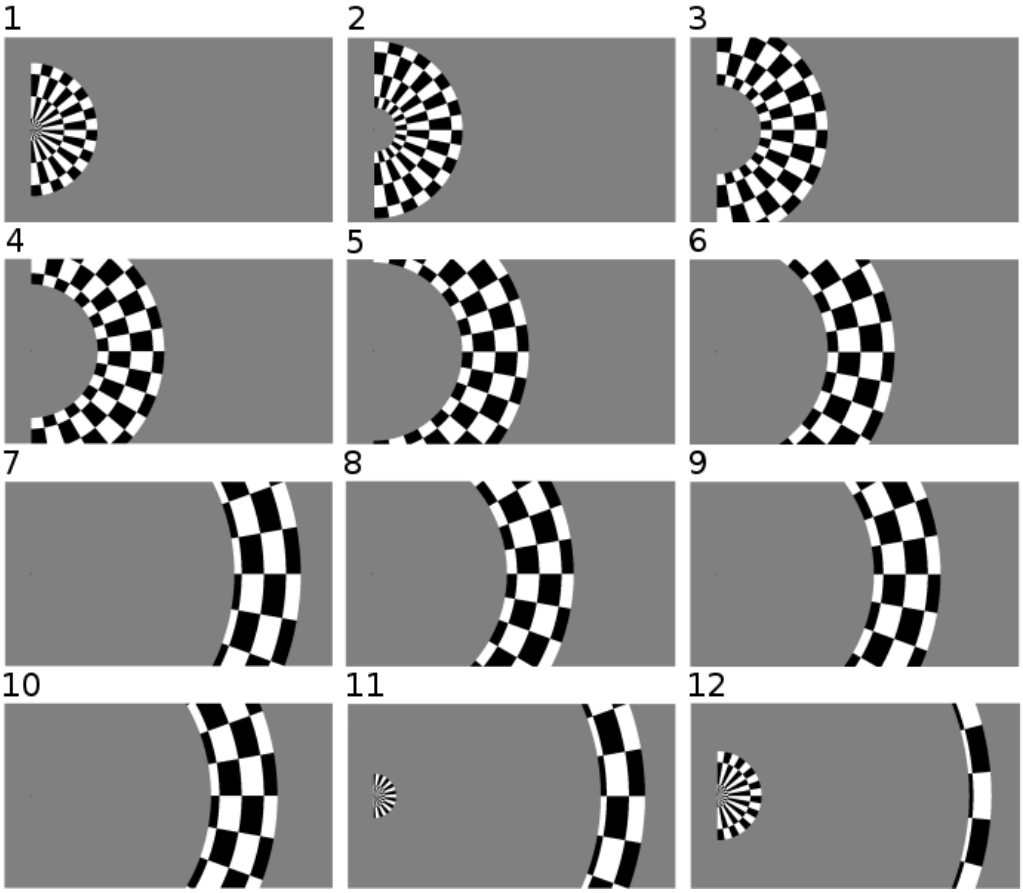

Figure A.3 – All frames representing the 12 steps of the expanding ring frames used to map the right hemifield. Each hemifield was tested separately, with the fixation cross placed 36 °on either the left or right side of the screen. All stimulus counterphase-flickered at 4 Hz and extended from fixation to 72 ° of visual field angle. The stimuli are based on the original retinotopic mapping stimuli used by Wandell et al. (2007).

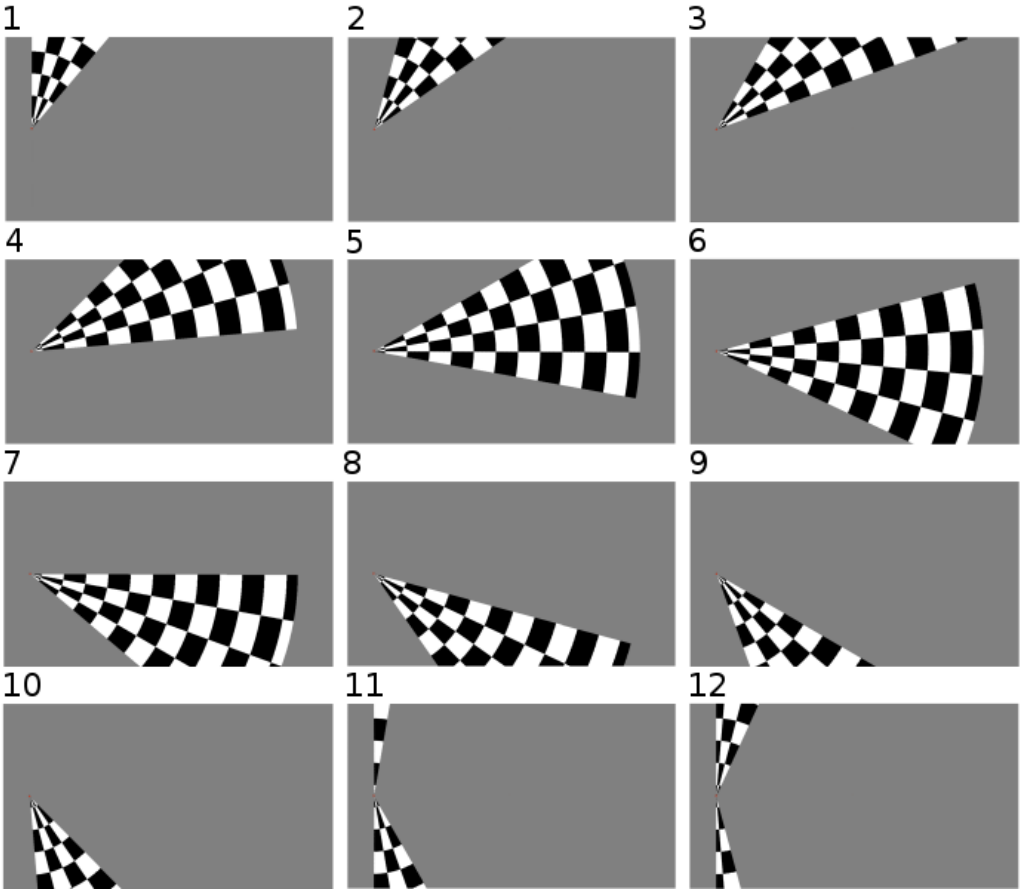

Figure A.4 – All frames representing the 12 steps of the expanding ring frames used to map the right hemifield. Each hemifield was tested separately, with the fixation cross placed 36 °on either the left or right side of the screen. All stimulus counterphase-flickered at 4 Hz and extended from fixation to 72 ° of visual field angle. The stimuli are based on the original retinotopic mapping stimuli used by Wandell et al. (2007).

A.2 Left and Right Hemifield Global Motion Data

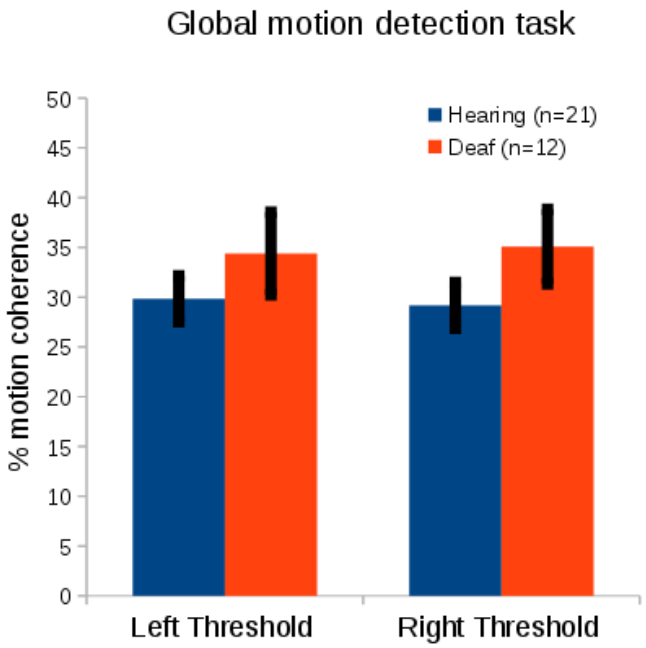

Figure A.5 – A bar graph which represents global motion discrimination task thresholds with the left and right hemifield conditions, angular and radial motion conditions averaged, which represent the percentage of coherently moving dots necessary for response accuracy of 75%. Plotted means of deaf and hearing groups. Error bars represent 1+/- SEM.

A.3 Spread of Results in Global and Local Motion Tasks

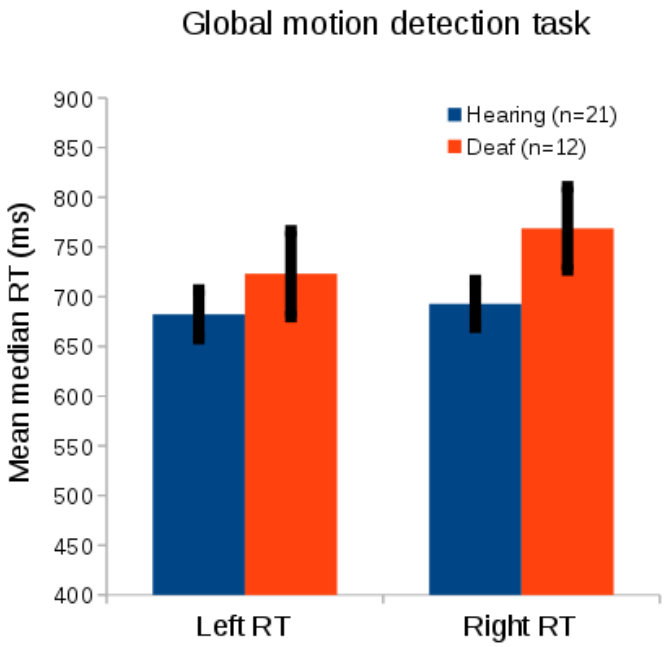

Figure A.6 – Global motion discrimination task reaction times plotted for the left and right hemifield conditions, angular and radial motion conditions averaged, which represent the reaction times necessary for response accuracy of 75%. Plotted means of deaf and hearing groups. Error bars represent 1+/- SEM.

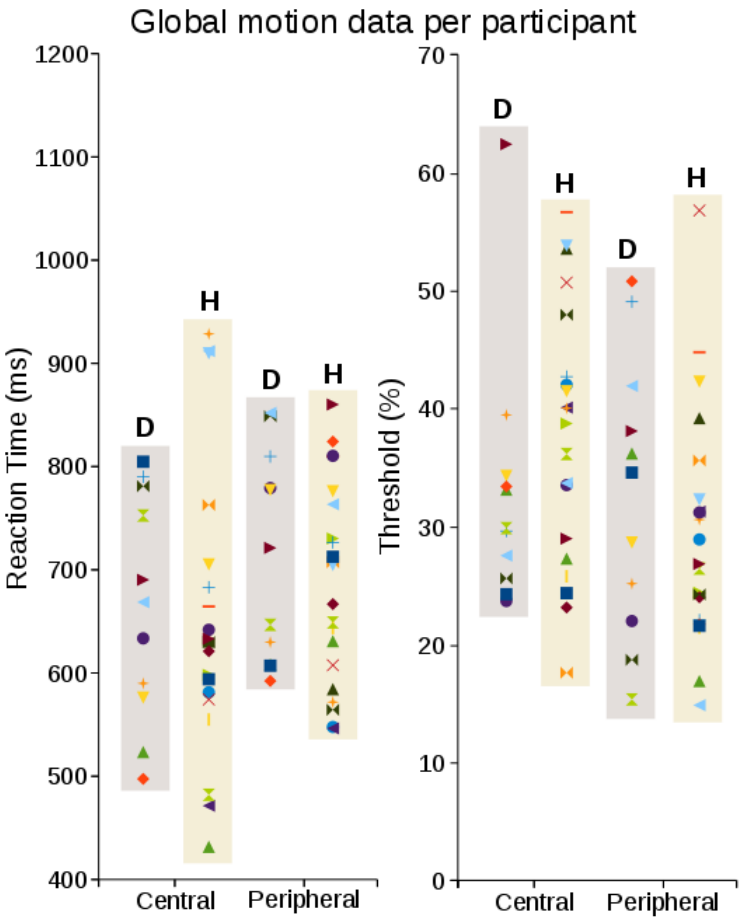

Figure A.7 – Global motion discrimination task reaction times to the left and the perceptual thresholds plotted to the right per subject, and divided into groups, where the angular and radial motion conditions were averaged. The threshold represents the percentage of coherently moving dots the necessary response time for a response accuracy of 75%, and the reaction time the speed of response also necessary for a response accuracy of 75%.

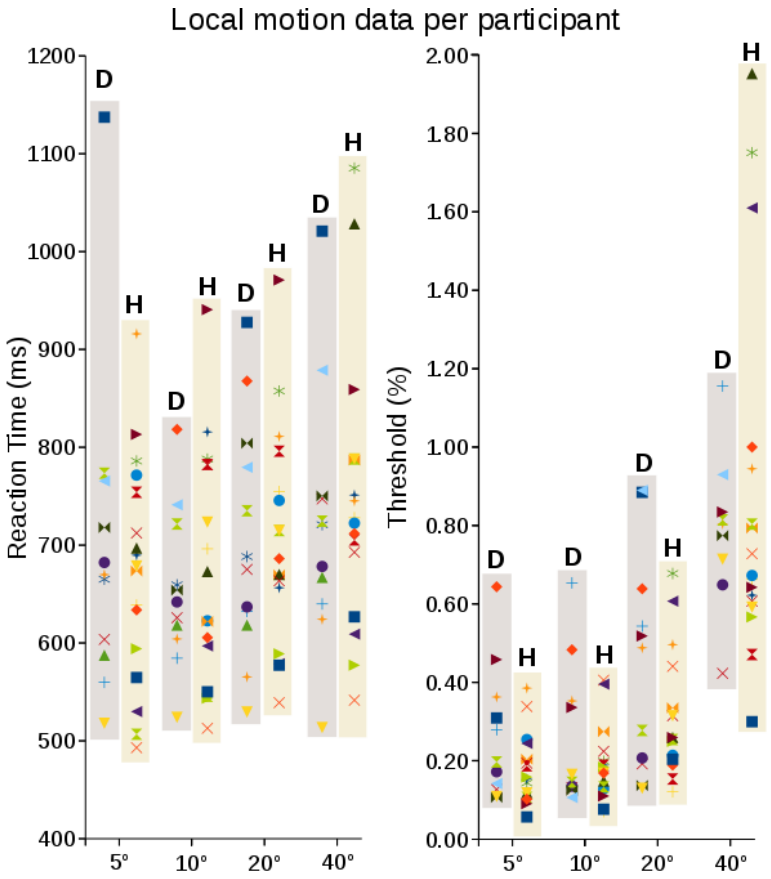

Figure A.8 – Local motion detection task reaction times to the left and the perceptual thresholds plotted to the right per subject, and divided into groups, where each eccentricity condition was averaged. The threshold represents the minimum speed at which motion was detected with an accuracy of 75%, and the reaction time the speed of response also necessary for a response accuracy of 75% .

Bibliography

Allen, J. S., Emmorey, K., Bruss, J., and Damasio, H. (2013). Neuroanatomical differences in visual, motor, and language cortices between congenitally deaf signers, hearing signers, and hearing non-signers. *Frontiers in neuroanatomy*, 7:26.

Amano, K., Wandell, B. A., and Dumoulin, S. O. (2009). Visual field maps, population receptive field sizes, and visual field coverage in the human MT+ complex. *Journal of neurophysiology*, 102(5):2704–2718.

Andrews, T. J., Halpern, S. D., and Purves, D. (1997). Correlated size variations in human visual cortex, lateral geniculate nucleus, and optic tract. *The Journal of neuroscience*, 17:2859–2868.

Armstrong, B. A., Neville, H. J., Hillyard, S. A., and Mitchell, T. V. (2002). Auditory deprivation affects processing of motion, but not color. *Cognitive Brain Research*, 14(3):422–434.

Barone, P., Lacassagne, L., and Kral, A. (2013). Reorganization of the connectivity of cortical field DZ in congenitally deaf cat. *PloS one*, 8(4):e60093.

Bartels, A., Logothetis, N. K., and Moutoussis, K. (2008). fMRI and its interpretations: an illustration on directional selectivity in area V5/MT. *Trends in Neurosciences*, 31(9):444–453.

Baumgart, F., Gaschler-Markefski, B., Woldorff, M. G., Heinze, H. J., and Scheich, H. (1999). A movement-sensitive area in auditory cortex. *Nature*, 400(6746):724–726.

Bavelier, D., Brozinsky, C., Tomann, A., Mitchell, T., Neville, H., and Liu, G. (2001). Impact of early deafness and early exposure to sign language on the cerebral organization for motion processing. *The Journal of neuroscience*, 21(22):8931–42.

Bavelier, D., Dye, M. W. G., and Hauser, P. C. (2006). Do deaf individuals see better? *Trends in Cognitive Sciences*, 10(11):512–518.

Bavelier, D., Green, C. S., Pouget, A., and Schrater, P. (2012). Brain plasticity through the life span: learning to learn and action video games. *Annual Reviews of Neuroscience*, 35:391–416.

Bavelier, D., Levi, D. M., Li, R. W., Dan, Y., and Hensch, T. K. (2010). Removing brakes on adult brain plasticity: from molecular to behavioral interventions. *The Journal of neuroscience*, 30(45):14964–14971.

Bavelier, D., Tomann, A., Hutton, C., Mitchell, T., Corina, D., Liu, G., and Neville, H. (2000). Visual attention to the periphery is enhanced in congenitally deaf individuals. *The Journal of neuroscience*, 20(17):RC93.

Beaudot, W. H. A. (2009). Psykinematix: A New Psychophysical Tool for Investigating Visual Impairment due to Neural Dysfunctions. *Vision*, 21(1):19–32.

Benson, N. C., Butt, O. H., Datta, R., Radoeva, P. D., Brainard, D. H., and Aguirre, G. K. (2012). The retinotopic organization of striate cortex is well predicted by surface topology. *Current Biology*, 22(21):2081–2085.

Billington, J., Furlan, M., and Wann, J. (2013). Cortical responses to congruent and incongruent stereo cues for objects on a collision path with the observer. *Displays*, 34(2):114–119.

Billino, J., Bremmer, F., and Gegenfurtner, K. R. (2008). Differential aging of motion processing mechanisms: Evidence against general perceptual decline. *Vision Research*, 48(10):1254–1261.

Bola, Ł., Zimmermann, M., Mostowski, P., Jednoróg, K., Marchewka, A., Rutkowski, P., and Szwed, M. (2016). Task-specific reorganization of the auditory cortex in deaf humans. *Proceedings of the National Academy of Sciences*, 114(4):600–609.

Bosworth, R. G. and Dobkins, K. R. (2002). The effects of spatial attention on motion processing in deaf signers, hearing signers, and hearing nonsigners. *Brain and cognition*, 49(1):152–169.

Bosworth, R. G., Petrich, J. A. F., and Dobkins, K. R. (2013). Effects of attention and laterality on motion and orientation discrimination in deaf signers. *Brain and Cognition*, 82(1):117–126.

Bosworth, R. G., Wright, C. E., Bartlett, M. S., Corina, D., and Dobkins, K. R. (2000). Characterization of visual properties of spatial frequency and speed in american sign language. *Cross-linguistic perspectives in sign language research:Selected papers from TISLR 2000*, 265–282.

Bottari, D., Caclin, A., Giard, M. H., and Pavani, F. (2011). Changes in early cortical visual processing predict enhanced reactivity in deaf individuals. *PLoS ONE*, 6.

Bottari, D., Heimler, B., Caclin, A., Dalmolin, A., Giard, M.-H., and Pavani, F. (2014). Visual change detection recruits auditory cortices in early deafness. *NeuroImage*, 94, 172-184.

Bottari, D., Valsecchi, M., and Pavani, F. (2012). Prominent reflexive eye-movement orienting associated with deafness. *Cognitive Neuroscience*, 3(1):8–13.

Braddick, O. J., O'Brien, J. M. D., Wattam-Bell, J., Atkinson, J., Hartley, T., and Turner, R. (2001). Brain areas sensitive to coherent visual motion. *Perception*, 30(1):61–72.

Brennan, M. and Bally, S. J. (2007). Psychosocial adaptations to dual sensory loss in middle and late adulthood. *Trends in amplification*, 11(4):281–300.

Brewer, A. and Barton, B. (2012). Visual field map organization in human visual cortex BT - Visual Cortex: Current Status and Perspectives. *Visual Cortex: Current Status and Perspectives*, (2):29–60.

Bridge, H., von dem Hagen, E. A. H., Davies, G., Chambers, C., Gouws, A., Hoffmann, M., and Morland, A. B. (2014). Changes in brain morphology in albinism reflect reduced visual acuity. *Cortex*, 56:64–72.

Bross, M. (1979). Residual Sensory Capacities of the Deaf: a Signal Detection Analysis of a Visual Discrimination Task. *Perceptual and Motor Skills*, 48(1):187–194.

Buckley, D., Codina, C., Bhardwaj, P., and Pascalis, O. (2010). Action video game players and deaf observers have larger Goldmann visual fields. *Vision research*, 50(5):548–556.

Burnat, K. (2015). Are visual peripheries forever young? *Neural Plasticity*, 2015:1–28.

Cardin, V., Hemsworth, L., and Smith, A. T. (2012a). Adaptation to heading direction dissociates the roles of human MST and V6 in the processing of optic flow. *Journal of Neurophysiology*, 108(3):794–801.

Cardin, V., Orfanidou, E., Rönnberg, J., Capek, C. M., Rudner, M., and Woll, B. (2013). Dissociating cognitive and sensory neural plasticity in human superior temporal cortex. *Nature Communications*, 4:1473.

Cardin, V., Sherrington, R., Hemsworth, L., and Smith, A. T. (2012b). Human V6: Functional Characterisation and Localisation. *PLoS ONE*, 7(10):e47685.

Cardin, V. and Smith, A. T. (2011). Sensitivity of human visual cortical area V6 to stereoscopic depth gradients associated with self-motion. *Journal of neurophysiology*, 106(3):1240–1249.

Cardin, V., Smittenaar, R. C., Orfanidou, E., Rönnberg, J., Capek, C. M., Rudner, M., and Woll, B. (2016). Differential activity in Heschl's gyrus between deaf and hearing individuals is due to auditory deprivation rather than language modality. *NeuroImage*, 124:96–106.

Cleland, B. G. and Levick, W. R. (1974). Brisk and sluggish concentrically organized ganglion cells in the cat's retina. *The Journal of Physiology*, 240(2):421–456.

Codina, C., Buckley, D., Port, M., and Pascalis, O. (2011a). Deaf and hearing children: A comparison of peripheral vision development. *Developmental Science*, 14(4):725–737.

Codina, C., Pascalis, O., Mody, C., Toomey, P., Rose, J., Gummer, L., and Buckley, D. (2011b). Visual advantage in deaf adults linked to retinal changes. *PLoS ONE*, 6(6):e20417.

Codina, C. J., Pascalis, O., Baseler, H. A., Levine, A. T., and Buckley, D. (2017). Peripheral visual reaction time is faster in deaf adults and British Sign Language interpreters than in hearing adults. *Frontiers in Psychology*, 8(FEB):1–10.

Connolly, M. and Van Essen, D. (1984). The representation of the visual field in parvicellular and magnocellular layers of the lateral geniculate nucleus in the macaque monkey. *The Journal of comparative neurology*, 226:544–564.

Cowey, A. and Rolls, E. T. (1974). Human cortical magnification factor and its relation to visual acuity. *Experimental brain research. Experimentelle Hirnforschung. Experimentation cerebrale*, 21:447–454.

Dale, A. M., Fischl, B., and Sereno, M. I. (1999). Cortical surface-based analysis. I. Segmentation and surface reconstruction. *NeuroImage*, 9(2):179–194.

DeYoe, E. A., Carman, G. J., Bandettini, P., Glickman, S., Wieser, J., Cox, R., Miller, D., and Neitz, J. (1996). Mapping striate and extrastriate visual areas in human cerebral cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 93(6):2382–2386.

Di Russo, F., Pitzalis, S., Spitoni, G., Aprile, T., Patria, F., Spinelli, D., and Hillyard, S. A. (2005). Identification of the neural sources of the pattern-reversal vep. *Neuroimage*, 24(3):874–886.

Dick, F., Taylor Tierney, A., Lutti, A., Josephs, O., Sereno, M. I., and Weiskopf, N. (2012). In Vivo Functional and Myeloarchitectonic Mapping of Human Primary Auditory Areas. *Journal of Neuroscience*, 32(46):16095–16105.

Dougherty, R. F., Koch, V. M., Brewer, A. A., Fischer, B., Modersitzki, J., and Wandell, B. A. (2003). Visual field representations and locations of visual areas V1/2/3 in human visual cortex. *Journal of vision*, 3:586–598.

Draganski, B., Gaser, C., Busch, V., Schuierer, G., Bogdahn, U., and May, A. (2004). Neuroplasticity: changes in grey matter induced by training. *Nature*, 427(6972):311–312.

Duhamel, J. R., Colby, C. L., and Goldberg, M. E. (1998). Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *Journal of neurophysiology*, 79(1):126–136.

Dumoulin, S. O., Bittar, R. G., Kabani, N. J., Baker, C. L., Le Goualher, G., Bruce Pike, G., and Evans, A. C. (2000). A new anatomical landmark for reliable identification of human area V5/MT: a quantitative analysis of sulcal patterning. *Cerebral cortex*, 10:454–463.

Dumoulin, S. O. and Wandell, B. A. (2008). Population receptive field estimates in human visual cortex. *NeuroImage*, 39(2):647–660.

Duncan, R. O. and Boynton, G. M. (2003). Cortical magnification factor in human primary visual cortex correlates with Vernier acuity thresholds. *Neuron*, 38(4), 659-671.

Dye, M. W. G., Hauser, P. C., and Bavelier, D. (2009). Is visual selective attention in deaf individuals enhanced or deficient? The case of the useful field of view. *PloS one*, 4(5):e5640.

Eickhoff, S. B., Paus, T., Caspers, S., Grosbras, M. H., Evans, A. C., Zilles, K., and Amunts, K. (2007). Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. *NeuroImage*, 36(3):511–521.

Elbert, T., Sterr, A., Rockstroh, B., Pantev, C., Müller, M. M., and Taub, E. (2002). Expansion of the tonotopic area in the auditory cortex of the blind. *The Journal of neuroscience*, 22(22):9941–9944.

Engel, S. A., Glover, G. H., and Wandell, B. A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cerebral Cortex*, 7:181–192.

Falchier, A., Clavagnier, S., Barone, P., and Kennedy, H. (2002). Anatomical evidence of multimodal integration in primate striate cortex. *The Journal of neuroscience*, 22:5749–5759.

Fattori, P., Breveglieri, R., Marzocchi, N., Filippini, D., Bosco, A., and Galletti, C. (2009a). Hand orientation during reach-to-grasp movements modulates neuronal activity in the medial posterior parietal area V6A. *The Journal of neuroscience*, 29:1928–1936.

Fattori, P., Pitzalis, S., and Galletti, C. (2009b). The cortical visual area V6 in macaque and human brains. *Journal of Physiology Paris*, 103(1-2):88–97.

Felleman, D. J. and Van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1(1):1–47.

Fine, I., Finney, E. M., Boynton, G. M., and Dobkins, K. R. (2005). Comparing the effects of auditory deprivation and sign language within the auditory and visual cortex. *Journal of cognitive neuroscience*, 17(2001):1621–1637.

Finney, E. M. (2001). Visual stimuli activate auditory cortex in the deaf. *Nature Neuroscience*, 4(12):1171.

Finney, E. M., Clementz, B. A., Hickok, G., and Dobkins, K. R. (2003). Visual stimuli activate auditory cortex in deaf subjects: evidence from MEG. *Neuroreport*, 14(11):1425–7.

Finney, E. M. and Dobkins, K. R. (2001). Visual contrast sensitivity in deaf versus hearing populations: Exploring the perceptual consequences of auditory deprivation and experience with a visual language. *Cognitive Brain Research*, 11:171–183.

Fischl, B. and Dale, A. M. (2000). Measuring the thickness of the human cerebral cortex from magnetic resonance images. *Proceedings of the National Academy of Sciences*, 97(20):11050–11055.

Fischl, B., Sereno, M. I., Tootell, R. B. H., and Dale, A. M. (1999). High-resolution inter-subject averaging and a surface-based coordinate system. *Human Brain Mapping*, 8(FEBRUARY 1999):272–284.

Freeman, J., Ziemba, C. M., Heeger, D. J., Simoncelli, E. P., and Movshon, J. A. (2013). A functional and perceptual signature of the second visual area in primates. *Nature neuroscience*, 16(7):974–81.

Galletti, C., Fattori, P., Gamberini, M., and Kutz, D. F. (1999). The cortical visual area V6: Brain location and visual topography. *European Journal of Neuroscience*, 11(11):3922–3936.

Galletti, C., Gamberini, M., Kutz, D. F., Fattori, P., Luppino, G., and Matelli, M. (2001). The cortical connections of area V6: An occipito-parietal network processing visual information. *European Journal of Neuroscience*, 13(8):1572–1588.

Gibson, E. J. (1969). Principles of perceptual learning and development., Appleton-Century-Crofts.

Giraud, A. L. and Lee, H. J. (2007). Predicting cochlear implant outcome from brain organisation in the deaf. *Restorative neurology and neuroscience*, 25(3-4):381–390.

Glasser, M. F. and Van Essen, D. C. (2011). Mapping human cortical areas in vivo based on myelin content as revealed by t1- and t2-weighted MRI. *The Journal of neuroscience*, 31:11597–11616.

Gougoux, F., Lepore, F., Lassonde, M., Voss, P., Zatorre, R. J., and Belin, P. (2004). Pitch discrimination in the early blind: People blinded in infancy have sharper listening skills than those who lost their sight later. *Nature*, 430 (6997):309.

Greco, V., Frijia, F., Mikellidou, K., Montanaro, D., Farini, A., D'Uva, M., Poggi, P., Pucci, M., Sordini, A., Morrone, M. C., and Burr, D. C. (2015). A low-cost and versatile system for projecting wide-field visual stimuli within fMRI scanners. *Behavior Research Methods*, 48(2):614–620.

Green, C. S. and Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature*, 423(6939):534–537.

Griffiths, T. D., Rees, G., Rees, A., Green, G. G. R., Witton, C., Rowe, D., Büchel, C., Turner, R., and Frackowiak, R. S. J. (1998). Right parietal cortex is involved in the perception of sound movement in humans. *Nature neuroscience*, 1(1):74–79.

Hackett, T. A. (2011). Information flow in the auditory cortical network. *Hearing Research*, 271(1-2):133–146.

Hackett, T. A., Preuss, T. M., and Kaas, J. H. (2001). Architectonic identification of the core region in auditory cortex of macaques, chimpanzees, and humans. *Journal of Comparative Neurology*, 441(3):197–222.

Harvey, B. M. and Dumoulin, S. O. (2011). The Relationship between Cortical Magnification Factor and Population Receptive Field Size in Human Visual Cortex: Constancies in Cortical Architecture. *Journal of Neuroscience*, 31(38):13604–13612.

Hauthal, N., Sandmann, P., Debener, S., and Thome, J. D. (2013). Visual movement perception in deaf and hearing individuals. *Advances in Cognitive Psychology*, 9:53–61.

Heffner, R. S. and Heffner, H. E. (1992). Sound localization in mammals. *The Evolutionary Biology of Hearing*, 232:691–715.

Heimler, B. and Pavani, F. (2014). Response speed advantage for vision does not extend to touch in early deaf adults. *Experimental Brain Research*, 232:1335–1341.

Hensch, T. K. (2005). Critical period plasticity in local cortical circuits. *Nature reviews. Neuroscience*, 6(11):877–888.

Hubel, D. H. and Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of physiology*, 160(1):106–154.

Huk, A. C., Dougherty, R. F., and Heeger, D. J. (2002). Retinotopy and functional subdivision of human areas MT and MST. *The Journal of neuroscience*, 22(16):7195–7205.

James, W. (1890). *The Principles of Psychology*. Read Books Ltd.

Karns, C. M., Dow, M. W., and Neville, H. J. (2012). Altered Cross-Modal Processing in the Primary Auditory Cortex of Congenitally Deaf Adults: A Visual-Somatosensory fMRI Study with a Double-Flash Illusion. *Journal of Neuroscience*, 32(28):9626–9638.

Knudsen, E. I. (2004). Sensitive Periods in the Development of the Brain and Behavior. *Journal of Cognitive Neuroscience*, 16(8):1412–1425.

Kolster, H., Peeters, R., and Orban, G. A. (2010). The Retinotopic Organization of the Human Middle Temporal Area MT/V5 and Its Cortical Neighbors. *Journal of Neuroscience*, 30(29):9801–9820.

Kontsevich, L. L. and Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Research*, 39(16):2729–2737.

Levi, D. M., Klein, S. A., and Aitsebaomo, A. P. (1985). Vernier acuity, crowding and cortical magnification. *Vision Research*, 25:963–977.

Livingstone, M. S. and Hubel, D. H. (1988). Do the relative mapping densities of the magno- and parvocellular systems vary with eccentricity? *The Journal of neuroscience*, 8(11):4334–9.

Loke, W. H. and Song, S. (1991). Central and peripheral visual processing in hearing and nonhearing individuals. *Bulletin of the Psychonomic Society*, 29(5):437–440.

Lomber, S. S. G. S. G., Meredith, M. A. A., and Kral, A. (2010). Cross-modal plasticity in specific auditory cortices underlies visual compensations in the deaf. *Nature neuroscience*, 13(11):1421–1427.

Macaluso, E. and Driver, J. (2005). Multisensory spatial interactions: A window onto functional integration in the human brain. *Trends in Neurosciences*, 28(5):264–271.

Malikovic, A., Amunts, K., Schleicher, A., Mohlberg, H., Eickhoff, S. B., Wilms, M., Palomero-Gallagher, N., Armstrong, E., and Zilles, K. (2007). Cytoarchitectonic analy-

sis of the human extrastriate cortex in the region of V5/MT+: A probabilistic, stereotaxic map of area hOc5. *Cerebral Cortex*, 17(3):562–574.

Marcar, V. L., Raiguel, S. E., Xiao, D., and Orban, G. A. (2000). Processing of kinetically defined boundaries in areas V1 and V2 of the macaque monkey. *Journal of neurophysiology*, 84(6):2786–2798.

Maunsell, J. H. R. and Newsome, W. T. (1987). Visual Processing in Monkey Extrastriate Cortex. *Annual Review of Neuroscience*, 10(1):363–401.

McGurk, H. and Macdonald, J. (1976). Hearing lips and seeing voices. *Nature*, 264(5588):746–748.

McKee, S. P. and Nakayama, K. (1984). The detection of motion in peripheral visual field. *Vision Research*, 24:25-32.

Memmert, D., Simons, D. J., and Grimme, T. (2009). The relationship between visual attention and expertise in sports. *Psychology of Sport and Exercise*, 10(1):146–151.

Meredith, M. A., Kryklywy, J., McMillan, A. J., Malhotra, S., Lum-Tai, R., and Lomber, S. G. (2011). Crossmodal reorganization in the early deaf switches sensory, but not behavioral roles of auditory cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 108(21):8856–8861.

Morel, A., Garraghty, P., and Kaas, J. (1993). Tonotopic organization, architectonic fields, and connections of auditory cortex in macaque monkeys. *Journal of Comparative Neurology*, 335(3):437–459.

Morosan, P., Rademacher, J., Schleicher, A., Amunts, K., Schormann, T., and Zilles, K. (2001). Human primary auditory cortex: cytoarchitectonic subdivisions and mapping into a spatial reference system. *Neuroimage*, 13(4):684–701.

Muiños, M. and Ballesteros, S. (2013). Visuospatial attention and motor skills in kung fu athletes. *Perception*, 42(10):1043–1050.

Myklebust, H. R. (1960). The psychology of deafness: Sensory deprivation, learning, and adjustment. New York: Grune Stratton.

Nath, A. R. and Beauchamp, M. S. (2012). A neural basis for interindividual differences in the McGurk effect, a multisensory speech illusion. *NeuroImage*, 59(1):781–787.

Nestares, O. and Heeger, D. J. (2000). Robust multiresolution alignment of MRI brain volumes. *Magnetic Resonance in Medicine*, 43:705–715.

Neville, H. J. and Lawson, D. (1987). Attention to central and peripheral visual space in a movement detection task: An event-related potential and behavioral study. II. Congenitally deaf adults. *Brain research*, 405(2):253–267.

Paranis, I. (1983). Visual perceptual skills and deafness: A research review. *Journal of the Academy of Rehabilitative Audiology*, 16:148160.

Park, S. and Chun, M. M. (2009). Different roles of the parahippocampal place area (PPA) and retrosplenial cortex (RSC) in panoramic scene perception. *NeuroImage*, 47(4):1747–1756.

Pascual-Leone, A. and Walsh, V. (2001). Fast backprojections from the motion to the primary visual area necessary for visual awareness. *Science*, 292(5516):510–512.

Pénicaud, S., Klein, D., Zatorre, R. J., Chen, J. K., Witcher, P., Hyde, K., and Mayberry, R. I. (2013). Structural brain changes linked to delayed first language acquisition in congenitally deaf individuals. *NeuroImage*, 66:42–49.

Pitzalis, S., Fattori, P., Galletti (2013). The functional role of the medial motion area V6. *Frontiers in Behavioural Neuroscience*, 6(January):91.

Pitzalis, S., Galletti, C., Huang, R.-S., Patria, F., Committeri, G., Galati, G., Fattori, P., and Sereno, M. I. (2006). Wide-field retinotopy defines human cortical visual area v6. *The Journal of neuroscience*, 26(30):7962–7973.

Pitzalis, S., Sdoia, S., Bultrini, A., Committeri, G., Di Russo, F., Fattori, P., Galletti, C., and Galati, G. (2013). Selectivity to Translational Egomotion in Human Brain Motion Areas. *PLoS ONE*, 8(4):e60241.

Pitzalis, S., Sereno, M. I., Committeri, G., Fattori, P., Galati, G., Patria, F., and Galletti, C. (2010). Human V6: The medial motion area. *Cerebral Cortex*, 20(2):411–424.

Proksch, J. and Bavelier, D. (2002). Changes in the spatial distribution of visual attention after early deafness. *Journal of cognitive neuroscience*, 14(5):687–701.

Recanzone, G. H. (2003). Auditory influences on visual temporal rate perception. *Journal of neurophysiology*, 89(2):1078–1093.

Rettenbach, R., Diller, G., and Sireteanu, R. (1999). Do deaf people see better? Texture segmentation and visual search compensate in adult but not in juvenile subjects. *Journal of cognitive neuroscience*, 11:560–583.

Reynolds, H. N. (1993). Effects of foveal stimulation on peripheral visual processing and laterality in deaf and hearing subjects. *The American journal of psychology*, 106(4):523–540.

Rockland, K. S. and Ojima, H. (2003). Multisensory convergence in calcarine visual areas in macaque monkey. *International Journal of Psychophysiology*, 50(1-2):19–26.

Roder, B. and Neville, H. (2003). Developmental functional plasticity. *Handbook of neuropsychology*, 9:231–270.

Sadato, N., Okada, T., Honda, M., Matsuki, K. I., Yoshida, M., Kashikura, K. I., Takei, W., Sato, T., Kochiyama, T., and Yonekura, Y. (2005). Cross-modal integration and plastic changes revealed by lip movement, random-dot motion and sign languages in the hearing and deaf. *Cerebral Cortex*, 15(8):1113–1122.

Saito, H., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., and Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *The Journal of neuroscience*, 6(1):145–157.

Samar, V. J. and Berger, L. (2017). Does a flatter general gradient of visual attention explain peripheral advantages and central deficits in deaf adults? *Frontiers in Psychology*, 8(May):713.

Schwarzkopf, D. S. and Rees, G. (2013). Subjective Size Perception Depends on Central Visual Cortical Magnification in Human V1. *PLoS ONE*, 8(3).

Scott, G. D., Karns, C. M., Dow, M. W., Stevens, C., and Neville, H. J. (2014). Enhanced peripheral visual processing in congenitally deaf humans is supported by multiple brain regions, including primary auditory cortex. *Frontiers in human neuroscience*, 8(March):177.

Sereno, M. I., Dale, A. M., Reppas, J. B., Kwong, K. K., Belliveau, J. W., Brady, T. J., Rosen, B. R., and Tootell, R. B. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, 268(5212):889–893.

Seymour, J. L., Low, K. A., Maclin, E. L., Chiarelli, A. M., Mathewson, K. E., Fabiani, M., Gratton, G., and Dye, M. W. (2016). Reorganization of neural systems mediating peripheral visual selective attention in the deaf: An optical imaging study. *Hearing Research*, 343, 162–175.

Shiell, M. M., Champoux, F., and Zatorre, R. J. (2014). Enhancement of visual motion detection thresholds in early deaf people. *PloS one*, 9(2):e90498.

Shiell, M. M. and Zatorre, R. J. (2016). White Matter Structure in the right Planum Temporale Region Correlates with Visual Motion Detection Thresholds in Deaf People. *Hearing Research*, 343:6–13.

Shipp, S. and Zeki, S. (1989). The Organization of Connections between Areas V5 and V1 in Macaque Monkey Visual Cortex. *European Journal of Neuroscience*, 1(4):309–332.

Simoncelli, E. P., Heegert, D. J., and Heeger, D. J. (1998). A Model of Neuronal Responses in Visual Area MT. *Vision Research*, 38(5):743–761.

Sincich, L. C. and Horton, J. C. (2005). The circuitry of V1 and V2: Integration of Color, Form, and Motion. *Annual Review of Neuroscience*, 28(1):303–326.

Siuda-Krzywicka, K., Bola, Ł., Paplińska, M., Sumera, E., Jednoróg, K., Marchewka, A., Śliwińska, M. W., Amedi, A., and Szwed, M. (2016). Massive cortical reorganization in sighted braille readers. *Elife*, 5:e10762.

Smith, A. T., Wall, M. B., Williams, A. L., and Singh, K. D. (2006). Sensitivity to optic flow in human cortical areas MT and MST. *European Journal of Neuroscience*, 23:561–569.

Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., Bannister, P. R., De Luca, M., Drobnjak, I., Flitney, D. E., Niazy, R. K., Saunders, J., Vickers, J., Zhang, Y., De Stefano, N., Brady, J. M., and Matthews, P. M. (2004). Advances in functional and structural MR image analysis and implementation as FSL. *NeuroImage*, 23(SUPPL. 1):S208–19.

Smittenaar, C., MacSweeney, M., Sereno, M., and Schwarzkopf, D. (2016). Does Congenital Deafness Affect the Structural and Functional Architecture of Primary Visual Cortex? *The Open Neuroimaging Journal*, 10(1):1–19.

Song, C., Schwarzkopf, D. S., Kanai, R., and Rees, G. (2015). Neural population tuning links visual cortical anatomy to human visual perception. *Neuron*, 85(3):641–656.

Spence, C. (2011). Crossmodal correspondences: a tutorial review. *Attention, perception & psychophysics*, 73(4):971–995.

Stenbacka, L. and Vanni, S. (2007). fMRI of peripheral visual field representation. *Clinical Neurophysiology*, 118(6):1303–1314.

Stevens, C. and Neville, H. (2006). Neuroplasticity as a double-edged sword: deaf enhancements and dyslexic deficits in motion processing. *Journal of cognitive neuroscience*, 18:701–714.

Striem-Amit, E., Almeida, J., Belledonne, M., Chen, Q., Fang, Y., Han, Z., Caramazza, A., and Bi, Y. (2016). Topographical functional connectivity patterns exist in the congenitally, prelingually deaf. *Scientific Reports*, 6(February):29375.

Tadin, D., Silvanto, J., Pascual-Leone, A., and Battelli, L. (2011). Improved Motion Perception and Impaired Spatial Suppression following Disruption of Cortical Area MT/V5. *Journal of Neuroscience*, 31(4):1279–1283.

Tootell, R. B., Dale, A. M., Sereno, M. I., Malach, R., Dinu, M., Abbate, R., Gensini, G. F., Casini, A., and Sofi, F. (1996). New images from human visual cortex. *Trends.Neurosci.*, 19(February):481–489.

Tootell, R. B., Reppas, J. B., Kwong, K. K., Malach, R., Born, R. T., Brady, T. J., Rosen, B. R., and Belliveau, J. W. (1995). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J. Neurosci.*, 15(4):3215–3230.

Ungerleider, L. G. and Desimone, R. (1986). Cortical connections of visual area MT in the macaque. *The Journal of comparative neurology*, 248(2):190–222.

Vachon, P., Voss, P., Lassonde, M., Leroux, J. M., Mensour, B., Beaudoin, G., Bourgouin, P., and Lepore, F. (2013). Reorganization of the auditory, visual and multimodal areas in early deaf individuals. *Neuroscience*, 245:50–60.

von Pföstl, V., Stenbacka, L., Vanni, S., Parkkonen, L., Galletti, C., and Fattori, P. (2009). Motion sensitivity of human V6: A magnetoencephalography study. *NeuroImage*, 45(4):1253–1263.

Walsh, C. and Polley, E. H. (1985). The Topography of Ganglion Cell Production in the Cat's Retina. 5(3):741–750.

Wandell, B. a., Chial, S., and Backus, B. T. (2000). Visualization and measurement of the cortical surface. *Journal of cognitive neuroscience*, 12(5):739–752.

Wandell, B., Dumoulin, S. O., and Brewer, A. (2007). Visual field maps in human cortex. *Neuron*, 56(2):366–383.

Wang, L., Mruczek, R. E. B., Arcaro, M. J., and Kastner, S. (2015). Probabilistic Maps of Visual Topography in Human Cortex. *Cerebral Cortex*, 25(10):3911–3931.

Warren, P. A. and Rushton, S. K. (2009). Optic flow processing for the assessment of object movement during ego movement. *Current Biology*, 19(18):1555–1560.

Wu, J., Wang, B., Yang, J., Hikino, Y., Takahashi, S., Yan, T., Ohno, S., and Kanazawa, S. (2013). Development of a method to present wide-view visual stimuli in MRI for peripheral visual studies. *Journal of Neuroscience Methods*, 214(2):126–136.

Yan, T., Jin, F., He, J., and Wu, J. (2011). Development of a wide-view visual presentation system for visual retinotopic mapping during functional MRI. *Journal of Magnetic Resonance Imaging*, 33(2):441–447.

Yushkevich, P., Piven, J., Cody, H., and Ho, S. (2005). User-guided level set segmentation of anatomical structures with ITK-SNAP. *Neuroimage*, 31(3):1116–1128..

Zarfaty, Y., Nunes, T., and Bryant, P. (2004). The performance of young deaf children in spatial and temporal number tasks. *Journal of deaf studies and deaf education*, 9(3):315–326.

Zatorre, R. J., Bouffard, M., Ahad, P., and Belin, P. (2002). Where is 'where' in the human auditory cortex? *Nature neuroscience*, 5(9):905–9.

Zeki, S., McKeefry, D. J., Bartels, a., and Frackowiak, R. S. (1998). Has a new color area been discovered? *Nature neuroscience*, 1(5):335–336.

Zhang, Y., Brady, M., and Smith, S. (2001). Segmentation of brain MR images through a hidden Markov random field model and the expectation-maximization algorithm. *IEEE Transactions on Medical Imaging*, 20(1):45–57.

Zhou, H., Friedman, H. S., and Von Der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience*, 20(17):6594–6611.